Plant community composition and biodiversity of irrigated rice ecosystems in Vietnam and the Philippines

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Adapt the pace of Nature. Her secret is patience.

- Ralph Waldo Emerson

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Abbreviations

AIC	= Akaike Information Criterion
a.s.l.	= above sea level
c.f.	= compare [lat. *confer*]
C_{org}	= organic carbon
DCA	= detrended correspondence analysis
EC	= electrical conductivity
e.g.	= for example [lat. *exempli gratia*]
etc.	= and so on [lat. *et cetera*]
GLMM	= generalized linear mixed-effects model
H	= Shannon diversity
i.e.	= that means [lat. *id est]*
incl	= including
LME	= linear mixed-effects
NMDS	= Nonmetric multidimensional scaling
N_{total}	= total nitrogen
PH	= Philippines
S	= species richness
SD	= standard deviation
S_{ipo}	= number of entomophilous (i.e. insect-pollinated) plants
spec.	= species
spp.	= several species [lat. *species pluralis*]
ssp.	= subspecies
UPGMA	= Unweighted Pair Group Method with Arithmetic Mean
VIF	= variance inflation factor
VN	= Vietnam

Summary

Irrigated rice landscapes in tropical and subtropical Asia are complex agroecosystems that have evolved mostly from natural wetlands. Millennia of interaction between human communities and their surrounding ecosystems have shaped these highly-dynamic and diverse environments that provide several valuable ecosystem services and host a diversity of plants, animals and habitats. However, this biodiversity is threatened by ongoing agricultural intensification and the conversion of vast farmland areas to monoculture crop production. Besides, the knowledge on the diversity and composition of plants in rice ecosystems and the occurring rice weed communities is still inadequate. This thesis aimed at a more comprehensive understanding of the diversity, composition, dynamics and distribution of rice weed communities in important rice-producing regions of Southeast Asia. Research focused on seven regions in Vietnam and the Philippines which are greatly varied in terms of climate, edaphic conditions, landscape heterogeneity, agricultural management and biodiversity. I examined two major habitat types of rice ecosystems, i.e. paddies (the field proper) and bunds (or levees), to reveal their plant diversity, the prevailing life forms, the plant communities, and the main environmental drivers and phytogeographic patterns that shape these communities.

In the introductory chapter, the importance of rice ecosystems and the origin and history of rice cultivation are discussed. Further, I inform on the nature of these agroecosystems by providing details on the biology of the rice plant, the ecology and composition of rice environments, and the significance, diversity and control of rice weeds. The chapter ends with a closer look on the study area and the general description of applied methods.

The second and the third chapter give information on the composition of plant species and prevailing life forms on local paddies and bunds, respectively. The descriptions are complemented by recorded (and in the case of paddies also projected) levels of species richness to provide a comprehensive picture of the floristic diversity of the rice ecosystems in total, in each region, in uplands and lowlands, and in the two countries. The two studies identify the main rice weed communities in paddies and on bunds, and provide details on their differential species, geographic distribution, plant diversity, time

of emergence during the crop cycle, as well as the abiotic conditions under which they occurred.

In the fourth chapter, the effects and relative importance of abiotic conditions, habitat type and surrounding landscapes on the plot-level plant diversity (alpha diversity) in the seven study regions are investigated and presented in a comparative overview. Another main objective of the study in this chapter is the quantification and visualization of the species turnovers (beta diversity) across sampling sites, between paddies and their bunds, and between regions.

The fifth chapter summarizes the major findings of the thesis to highlight the differences and similarities of bunds and paddies in terms of floristic diversity, the composition of species and life forms, the community variation along environmental gradients, and applied weed control measures and cultivation practices. I conclude that our results provide new insights into the composition and functioning of rice landscapes, and indicate remaining issues. The findings offer interesting opportunities for biodiversity conservation, ecological engineering approaches and the sustainable management of rice ecosystems.

Zusammenfassung

Die bewässerten Reislandschaften im tropischen und subtropischen Asien stellen komplexe Agrarökosysteme dar, die zumeist aus natürlichen Feuchtgebieten hervorgegangen sind. Jahrtausendelange Interaktion zwischen menschlichen Gemeinschaften und den ihnen umgebenden Ökosystemen haben diese hoch-dynamischen und vielfältigen Umgebungen erschaffen, die einige wertvolle Ökosystemdienstleistungen bieten und eine Vielfalt an Pflanzen, Tieren und Habitaten beherbergen. Diese Biodiversität ist jedoch durch die fortschreitende Intensivierung der Landwirtschaft und die monokulturelle Verarmung großer agrarisch genutzter Landstriche gefährdet. Hinzu kommt, dass das Wissen über die Vielfalt und Zusammensetzung von Pflanzen in Reisökosystemen und die dort vorkommenden Reisunkrautgesellschaften immer noch lückenhaft ist. Diese Dissertation dient einem umfassenderen Verständnis der Diversität, Zusammensetzung, Dynamik und Verbreitung von Reisunkrautgesellschaften in bedeutenden Reisanbaugebieten Südostasiens. Die Studie konzentriert sich auf sieben Regionen in Vietnam und den Philippinen, die eine große Spannweite unterschiedlicher Klima- und Bodenverhältnisse, Landschaftsheterogenität, landwirtschaftlicher Bewirtschaftungspraktiken und Biodiversität aufweisen. Untersucht wurden zwei der wichtigsten Habitattypen in Reisökosystemen, Reisfelder und Reisfeldränder beziehungsweise -dämme, um deren Pflanzenvielfalt und die vorherrschenden Lebensformentypen, sowie ihrer Pflanzengemeinschaften und deren wichtigste bestimmende Umweltbedingungen und phytogeografischen Muster aufzudecken.

Im einleitenden Kapitel erörtere ich die Wichtigkeit von Reisökosystemen, sowie den Ursprung und die geschichtliche Entwicklung des Reisanbaus. Außerdem informiere ich über die Beschaffenheit dieser Agrarökosysteme mit Details zur Biologie der Reispflanze, der Ökologie und Zusammensetzung von Reisanbaugebieten, sowie der Bedeutung, Vielfalt und Bekämpfung von Reisunkräutern. Das Kapitel endet mit einer Einführung in das Untersuchungsgebiet und einer allgemeinen Beschreibung der angewandten Methodik.

Zweites und drittes Kapitel informieren über die Zusammensetzung der Pflanzenarten und der vorherrschenden Lebensformen auf den örtlichen Reisfeldern beziehungsweise

deren Rändern. Die Beschreibungen werden ergänzt durch Angaben zum erfassten (und im Fall der Reisfelder auch hochgerechneten) Artenreichtum um ein umfassendes Bild der floristischen Vielfalt der Reisökosysteme insgesamt, in den Regionen, im Hoch- und Tiefland, sowie in den beiden Ländern zu zeichnen. Die beiden Studien ermitteln die wichtigsten Reisunkrautgesellschaften der Reisfelder und deren Ränder und informieren über ihre Zeigerarten, ihre geografische Verbreitung, ihre Pflanzenvielfalt, dem Zeitpunkt ihres Erscheinens während des Reisanbauzyklus, sowie den abiotischen Bedingungen unter denen sie vorkamen.

Im vierten Kapitel werden der Einfluss und die relative Bedeutung der abiotischen Bedingungen, des Habitattyps und der umgebenden Landschaft auf die Pflanzenvielfalt der Untersuchungsflächen (Alpha-Diversität) in den sieben Untersuchungsregionen analysiert und in einer vergleichenden Übersicht dargestellt. Des Weiteren dient die hier vorgestellte Studie der Quantifizierung und Visualisierung der Unterschiede in der Artenzusammensetzung (Beta-Diversität) zwischen den Untersuchungsflächen, zwischen Reisfeldern und deren Rändern, sowie zwischen den Regionen.

Im fünften Kapitel werden die wichtigsten Ergebnisse der Dissertation zusammengefasst um die Unterschiede und Gemeinsamkeiten von Reisfeldern und deren Rändern im Hinblick auf deren floristische Diversität, Zusammensetzung der Arten und Lebensformen, der Veränderung der Pflanzengemeinschaften entlang von Umweltfaktoren, sowie der verwendeten Anbau- und Unkrautbekämpfungsmethoden aufzuzeigen. Daraus schließe ich, dass unsere Ergebnisse neue Erkenntnisse über die Zusammensetzung und das Funktionieren von Reislandschaften liefern, und weise auf noch offene Fragen hin. Die Erkenntnisse bieten interessante Möglichkeiten für den Schutz der Artenvielfalt, für Ansätze im Bereich des ‚Ecological Engineering' und für eine nachhaltige Bewirtschaftung der Reisanbaugebiete.

Chapter 1:

General introduction

1.1. The importance of rice ecosystems

Cultivated rice (*Oryza sativa* L.) is grown worldwide and has fed more people for a longer time than any other crop on Earth (GRiSP 2013). In 2018, rice was harvested on an area that extended over 162 million ha and 116 countries, and the production quantity exceeded 762 million tonnes, of which around 90% were produced in Asia and 33% in Southeast Asia, respectively (FAO 2020). Particularly in Asia and most developing countries, rice is the staple food and the main source of income and employment for rural people (GRiSP 2013). About 144 million farms and millions of hired day-laborers in Asia depend on rice production to make a living (FAO 2014). Products from rice are used as food, fodder, beverages, medicine, cosmetics, fuel, fertilizer, construction material etc. Rice is such an integral part of local life and culture that the question "Have you consumed rice yet?" is a common greeting in several Asian countries (e.g. Sowattanangoon et al. 2009; Piras 2011). Besides, rice ecosystems provide several ecosystem services and sustain a rich diversity of species and habitats (Edirisinghe & Bambaradeniya 2006; Burkhard et al. 2015).

1.2. Origin, history and current objectives of rice cultivation

The genus *Oryza* probably originated at least 130 million years ago and comprises nowadays two cultivated and 22 wild species of rice (Khush 1997; Sanchez et al. 2013). *Oryza sativa*, the Asian cultivated rice, is produced worldwide, whereas the African cultivated rice *O. glaberrima* is endemic to West Africa and grown only locally (Muthayya et al. 2014). The domestication of rice started with the split of *Oryza sativa* from its ancestor *O. rufipogon* in China and Southeast Asia about 8,000 to 13,500 years ago (Molina et al. 2011; Huang et al. 2012). The origins of rice cultivation have been long debated. Many believe that rice was directly seeded at first, without standing water, on forest clearings under a system of shifting cultivation (GRiSP 2013), whereas Ikehashi (2007) hypothesized that rice cultivation developed first via vegetative propagation by transplanting plants into shallow flooded marshes. Anthropogenic development and natural evolution have changed rice ecosystems immensely since the Neolithic era, and rice cultivation spread into other parts of the world. Probably around 330 B.C., the crop was introduced from Asia to Europe and northern Africa, spread onwards to America in the 17th century, came finally to Australia in the 20th century,

and is grown today on every continent except Antarctica (GRiSP 2013). These days, more than 90,000 rice varieties exist and over 132,000 accessions (including cultivated species of rice, wild relatives and species from related genera) are conserved in the International Rice Genebank on the Philippines (Evenson & Gollin 1997; IRRI 2018). Particularly since the 'Green Revolution' in the 1960s, high-yielding rice varieties, increased input of fertilizers, pesticides and water, new technologies and changing policies led to a rapid increase in productivity (Bouman et al. 2007a; Pingali 2012). The environmental, social and economic costs of these changes, such as declining agro-biodiversity, degradation of soils and water resources, increasing pest outbreaks, health damages of people and animals, increasing dependencies of farmers, and unstable yields, became apparent soon (Pretty 2002; Pingali 2012; Tekken & Settele 2014). More sustainable methods of rice production like the Integrated Pest Management (IPM), the System of Rice Intensification (SRI) or the salinity farming in Vietnam became known to a wider public since the 1980s (Pretty 2002). During the last decade, the FAO developed a regional strategy for rice production in Asia with following objectives: (1) increase the productivity and nutrition value of rice sustainably, (2) enhance the rice value chain and reduce post-harvest losses, (3) adapt rice farming to climate change, (4) minimize environmental impacts and enhance ecosystem functions of rice landscapes, (5) promote fair and efficient market and trade, and (6) improve organization of production, and empower youth and women (FAO 2014).

1.3. The nature of rice ecosystems

1.3.1. Biology of the rice plant *Oryza sativa* L.

Cultivated rice is generally considered as a semi-aquatic, annual grass of the family *Poaceae*, although it can survive as a perennial under favorable conditions. At maturity, the rice plant has a main stem and several tillers that can bear terminal panicles with single-flowered spikelets (GRiSP 2013). Rice is basically self-pollinated, but cross-pollination by wind or insects can occur (Pu et al. 2014). Plant height, number of tillers and growth time vary by rice variety and environmental conditions. Generally, the growth duration is 3–6 months, and plant height ranges from 0.4 m to more than 5 m in some floating rice (GRiSP 2013). The life history of rice can be divided into a vegetative phase (including germination, seedling stage and tillering stage), a reproductive phase (including panicle initiation, booting stage and flowering stage) and

a ripening phase (including milk stage, dough stage and mature stage; see Fig. 1.1) (Bambaradeniya & Amerasinghe 2003).

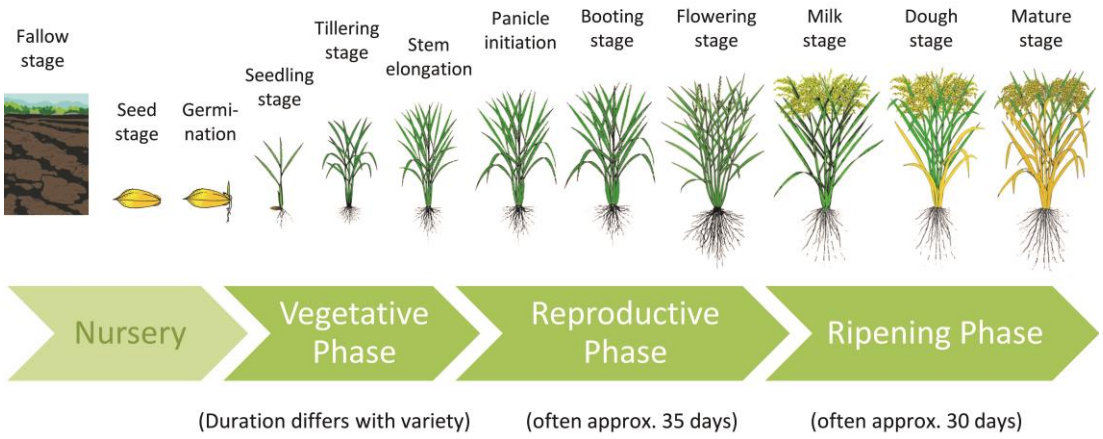

Fig. 1.1: The crop cycle of paddy rice from fallow stage to mature stage (adapted from IRRI 2020). Transplanting of plants from seedbeds to the field may take place during the seedling stage, harvest follows the ripening phase. Weeds are a serious concern for farmers until the booting stage.

1.3.2. Ecology and composition of rice ecosystems

Rice ecosystems are highly dynamic, artificial wetlands. Frequent disturbances by agricultural management and natural events (e.g. rainfall and flooding) lead to rapid physical, chemical, and biological changes (Bambaradeniya & Amerasinghe 2003).

Typical methods of land preparation before crop establishment are soaking, plowing, and puddling (harrowing under shallow submerged conditions; Fig. 1.2a, b) (IRRI 2020). Afterwards, rice is directly seeded or seedlings grown in a seedbed are transplanted onto the fields (Fig. 1.2c, d) (GRiSP 2013). Further farming practices are applied at different times and with varying intensity, e.g. irrigation, application of agrochemicals (fertilizers, pesticides) and weeding (Fig. 1.2e, f). Growth and yields are best in flooded soils, but rice is grown in a wide range of locations and under diverse conditions (De Datta 1981).

Fig. 1.2: Land preparation with (a) machinery is common at intensive lowland rice production sites, whereas (b) water buffalos are often used to harrow paddies in traditional low-input rice cultivation. Rice plants are grown in (c) seedbeds before (d) transplanting them onto the paddies. Weeds can be controlled directly via water management, (e) application of herbicides and (f) manual weeding (here with so-called 'weeder').

Based on hydrological characteristics, rice environments can be classified mainly in irrigated, rainfed and flood-prone ecosystems (Khush 1997; Bouman et al. 2007a; GRiSP 2013):

- **Irrigated** rice is grown in flooded paddy fields (in the following just called 'paddies') that are embanked with levees (or 'bunds') to keep them inundated during a major part of the crop season (Fig. 1.3, 1.5, 1.6). Supplementary irrigation is

common during the wet season but essential during the dry season. Bunds are temporarily broken at certain spots to provide fresh water flow from and to surrounding paddies. Paddy rice can be grown up to three times a year in irrigated lowland fields, whereas irrigated upland rice is harvested only once a year due to climatic conditions.

- **Rainfed** lowland fields are also bunded, but water supply depends entirely on the timing, duration and intensity of rainfall. Precipitation patterns range from short periods of rainfall with severe drought stress for the crop to water stagnation for 2–5 months. Rainfed upland rice is grown under highly heterogeneous conditions due to varying climate, soils, and topography. Shifting cultivation is still common in parts of the Asian upland rice area.
- **Flood-prone** ecosystems with floating or deepwater rice are found in large river deltas of South and Southeast Asia. These environments are subject to periods of uncontrolled deep flooding and excess of water during part of the growing season, with standing water depths varying from 0.5 m to 3 m.

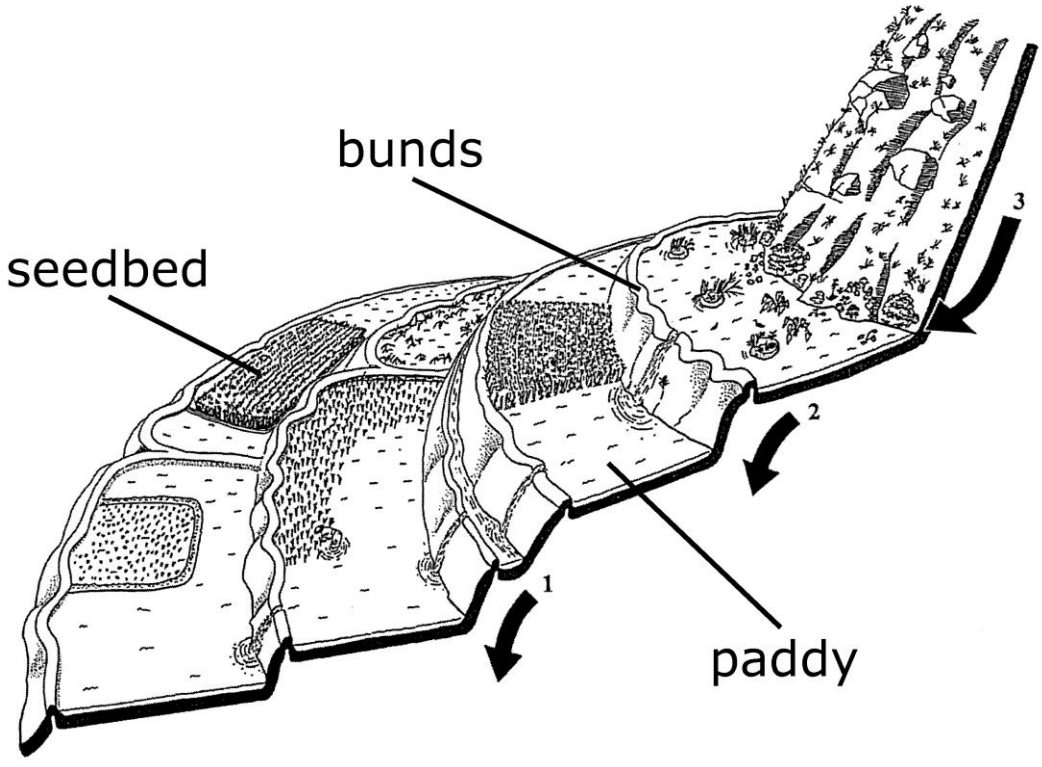

Fig. 1.3: Water supply in rice terraces of the traditional production system of Ifugao, Philippines: (1) from diverted brooks, (2) from field to field, and (3) with percolating spring water from the mountain side (adapted from Martin & Sauerborn 2013).

An exclusive feature of Asian rice cultivation in uplands are rice terraces on mountain slopes, e.g. in Ifugao Province, Philippines (Fig. 1.3, 1.4). The complex systems provide several ecosystem functions and services apart from rice production like the provisioning of diverse sources of food and medicine, water regulation and conservation, erosion reduction, and various cultural, ecological and socioeconomic values (Castonguay et al. 2016).

Fig. 1.4: View on the famous Batad rice terraces, a UNESCO World Heritage Site, in Ifugao Province, Philippines.

Irrigated lowland rice accounts for 75% of the global rice production (GRiSP 2013). Three main habitat types are differentiated in irrigated rice ecosystems (Bambaradeniya & Amerasinghe 2003): the paddy, the bund and the ditch (water supply canal) (Fig. 1.3, 1.5–7). Paddy shapes and sizes vary from small rice terraces of some square meters adapted to a mountain's topography to large rectangular fields of a few hectares in intensive monoculture areas in the lowlands. Paddy soils are greatly diversified in terms of chemistry, physics and biology, but common to all is a gley horizon (De Datta 1981). Bunds and ditches are mostly earthen but can also be constructed with concrete, and in the case of bunds also with gravel and stones (Huang et al. 2003; Fukamachi et al. 2005; Naito et al. 2012; Luo et al. 2014). Shapes and sizes of bunds and ditches vary as well with local site conditions. Rice terrace walls might represent another important habitat type exclusive to mountainous areas.

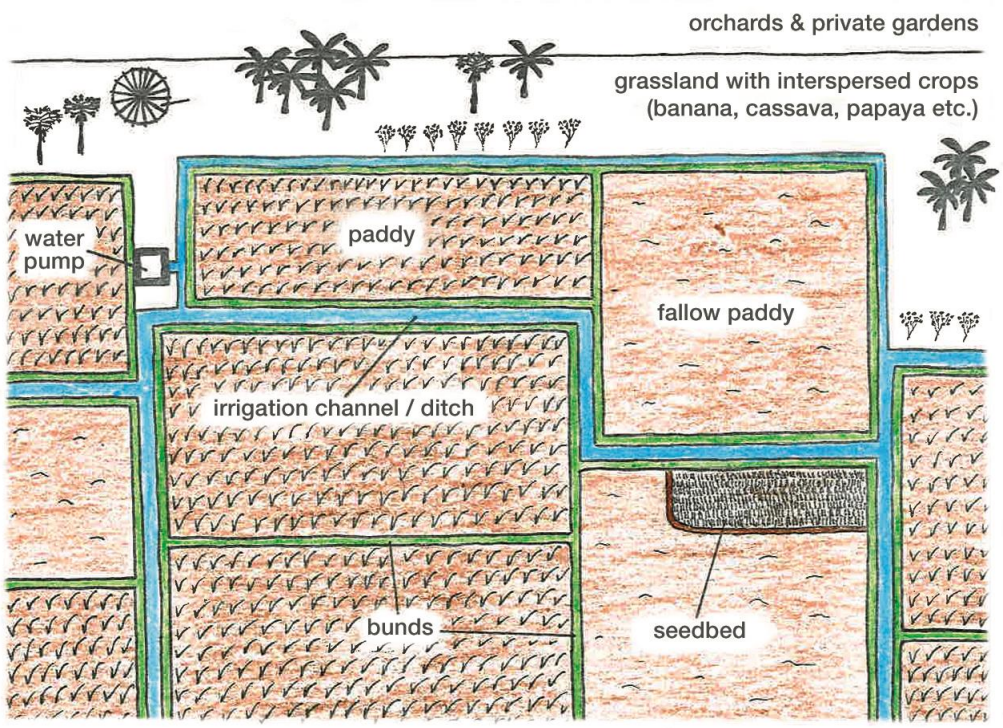

Fig. 1.5: Schematic picture of irrigated lowland rice fields.

The mosaic of temporary flooded fields, contiguous dry land and irrigation channels supports a diversity of microbes (pro- and eukaryotes), plants (algae, ferns, graminoids and herbs), fungi, invertebrates (insects, spiders, annelids, nematodes, mollusks, crustaceans), and vertebrates (fish, amphibians, reptiles, birds and mammals) (Bambaradeniya & Amerasinghe 2003). Population dynamics of the associated biota result from the spatial and temporal variability of environmental conditions during the cultivation cycle, which consists of an aquatic, semi-aquatic and terrestrial phase (Edirisinghe & Bambaradeniya 2006). The biological communities, with arthropods and plants as the most important components, serve as key indicators of the structural stability of rice ecosystems (Luo et al. 2014). Further, the biodiversity in rice landscapes provides valuable services like biological control, pollination, provisioning of food and medicine, aesthetical values etc., which led to concerns about its loss through modern agriculture since the 1990s (e.g. Way & Heong 1994; Edirisinghe & Bambaradeniya 2006; GRiSP 2013; Luo et al. 2014; Nguyen et al. 2018). Particularly in Southeast Asia, which is considered as a hotspot of species richness and endemism, biodiversity is seriously threatened by agricultural expansion and deforestation (Myers et al. 2000; Sodhi et al. 2010). Several studies have highlighted the complex biological interactions in rice environments, particularly between rice pests and their antagonists (e.g. Cohen et

al. 1994; Way & Heong 1994; Schoenly et al. 1996; Settle et al. 1996; Ali et al. 2019). A closer look on the flora associated with rice cultivation follows in chapter 1.3.3. Lately, ecological engineering approaches launched in Vietnamese villages have shown their potential for conserving natural habitats, augmenting biodiversity, and sparing farmers' money by planting nectar-rich flowers on bunds and cultivating rice without using insecticides (GRiSP 2013).

1.3.3. Rice weeds

The flora associated with rice ecosystems is mostly referred to as 'rice weeds'. These are mainly grasses, sedges and dicot herbs that compete with the crop for space, water, nutrients and light (Bambaradeniya & Amerasinghe 2003; Webster 2014). Rice weeds comprise native and alien plants, with different life forms and varied strategies of growth and reproduction. Most rice weeds are highly adaptable, fast growing C4 plants (Mahajan et al. 2014). More than 1,800 rice weeds have been recorded in South and Southeast Asia alone (Moody 1989), including a variety of globally rare species (IUCN 2015; Nowak et al. 2015). Some of the most common cosmopolitan rice weeds are weedy rice (a complex of taxonomically not well defined *Oryza* species, hybrids and biotypes), graminoids of the genera *Echinochloa* (mainly *E. colona* and *E. crus-galli*), *Cyperus* (mainly *C. difformis, C. iria* and *C. rotundus), Scirpus* (mainly *S. juncoides*), *Fimbristylis* (mainly *F. miliacea*), and *Leptochloa* (mainly *L. chinensis*), and herbs of the genera *Alisma*, *Heteranthera*, *Monochoria*, *Sagittaria* and *Amaranthus* (Kraehmer et al. 2016).

Rice weeds are strongly adapted to the phenology of rice, its environment and related agri- and sociocultural practices. The main habitat types of rice ecosystems are characterized by distinct weed communities (Bambaradeniya & Amerasinghe 2003): in ditches occur predominantly submergent, emergent, and floating hydrophytes, on bunds grow mostly terrestrial plants, while algae and weeds cope best with excess water stress in flooded paddies but are successively replaced by terrestrial weeds when fields are drained (Fig. 1.6). Many rice weeds grow in and along ditches (Kraehmer et al. 2016), and also the vegetation on bunds can be dense and speciose (e.g. Fukamachi et al. 2005; Kumalasari & Bergmeier 2014), whereas paddies are often sparsely covered with rather few species (Miyawaki 1960). Regional differences of the diversity and composition of the rice weed flora evolved due to geography and surrounding vegetation, climate,

edaphic conditions, rice cultivar and agricultural management (Yamada et al. 2011; Luo et al. 2014; Kraehmer et al. 2016). Rice weed communities from the Mediterranean (e.g. Bolòs & Masclans 1955; Piccoli & Gerdol 1981; García & Benzal 2009) and Asia (e.g. Miyawaki 1960; Kolbek et al. 1996; Kumalasari 2014; Nowak et al. 2015) have been described and classified since the 1950s.

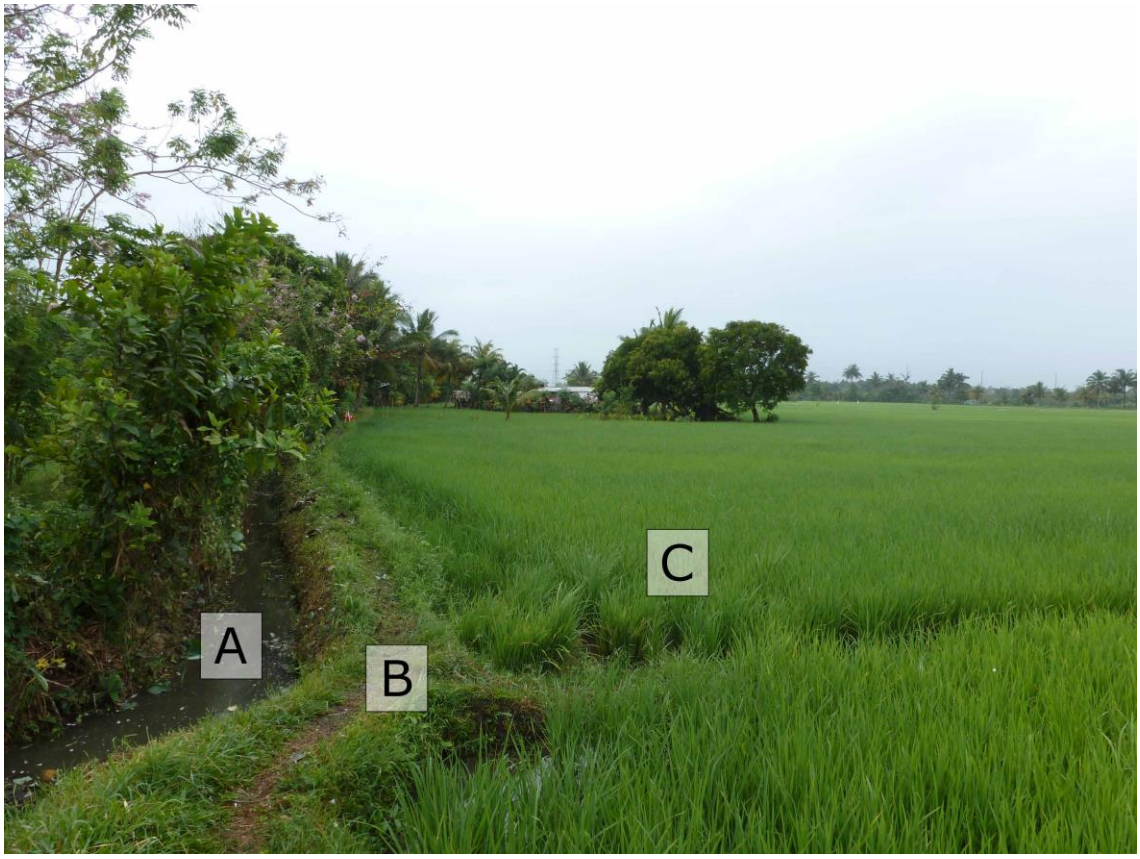

Fig. 1.6: Rice production site in Nacgarlan, Philippines. (A) Ditches, (B) bunds and (C) paddies are characterized by distinct weed communities.

Various studies have stressed the valuable services that the weed flora in rice ecosystems can provide, e.g. habitats and food for threatened species and beneficial species like rice pest antagonists and crop pollinators, and alternative food, medicine, and ornamental plants for trade or consumption (e.g. Way & Heong 1994; Edirisinghe & Bambaradeniya 2006; Kosaka et al. 2013; Naito et al. 2013; Luo et al. 2014; Nithya & Ramamoorthy 2015; Westphal et al. 2015; Ali et al. 2019). On the contrary, much research has been carried out to improve methods of weed control because rice weeds can severely constrain rice production by competition with the crop for nutrients, space, water and light, by serving as a host to diseases and pests, and by reducing the efficiency of irrigation and harvest (De Datta 1981). Oerke and Dehne (2004) estimated

that about 10% of the global rice production are lost due to weed infestations. Weed problems can be enhanced by continuous rice cultivation without crop rotation, direct-seeding of contaminated seeds, unwanted protection of weeds by insecticides and fungicides, development of herbicide resistance etc. (Kraehmer et al. 2016). A successful weed management strategy mostly combines mechanical, chemical and cultural management practices with a profound knowledge of the behavior and composition of weeds in the region (Webster 2014). Different direct and indirect weed control methods are applied in rice cultivation. Emergence and growth of weeds can be controlled indirectly via land preparation, rice cultivar, seed purity, fertilization technique, planting space and time, planting method (direct-seeding or transplanting), crop rotation, and biological control (De Datta 1981; Kumalasari 2014). Important direct weed control methods are:

- **Water management:** Mahajan et al. (2014) stressed that water management has a major impact on the infestation of weeds. Transplanting rice into standing water favors the growth of rice, but reduces the germination and establishment of weeds (Tuong et al. 2005). Rao et al. (2007) have listed several studies proofing the reduced growth and survival of weeds under flooded conditions. However, declining water availability leads to reduced irrigation of fields, and the development of more water-efficient technologies and production systems becomes increasingly important (Bouman et al. 2007b). Further, several major rice weeds, such as weedy rice, *Echinochloa* spp., *Cyperus* spp. or *Fimbristylis miliacea*, are tolerant to flooding (Kaspary et al. 2020).
- **Manual weeding / hand weeding:** Despite the increased use of herbicides, manual weeding is still common in almost all tropical rice-growing areas. It is basically done by pulling weeds with hands, but also simple mechanical equipment (e.g. hoe, modified trowel, machete, so-called ‘weeder’ etc.) is used (Fig. 1.2f). Manual weeding should not delay 42 days in transplanted rice, and 25 days in dry-seeded rice (De Datta 1981). The method can be highly effective, but it is limited by high labor costs, labor scarcity, weather conditions, and fragmentation with consequent regeneration of perennial weeds (Rao et al. 2007).
- **Herbicides:** Since the 1970s, manual weed control has been increasingly replaced by the use of herbicides as chemical weed control can save time, money, water and labor in the short term (Naylor 1994). Much research has been conducted on the

optimum rate, time, type, and method of herbicide application (Rao et al. 2007). Herbicides are applied in granular formulation, by spraying (Fig. 1.2e), or by sand mix application (Mahajan et al. 2014). Timing of herbicide application depends on the method of rice cultivation. For dry-seeded rice, Kim and Na (2005) generally recommended one herbicide application just before or after rice emergence and another one at the flood period. Preemergence herbicides are very effective in puddled transplanted rice when applied 4–7 days after transplanting but before weed emergence (Mahajan et al. 2014). Negative long-term side-effects of herbicide application are the evolution of herbicide resistance in weeds, and the deposition of toxic residues in the environment and in agricultural products (Kudsk & Streibig 2003).

1.4. A closer look on Vietnam and the Philippines

All presented studies of this thesis focus on the weed flora associated with irrigated rice ecosystems in Vietnam and the Philippines. The two countries are located in Southeast Asia (Fig. 1.7), both are biodiversity hotspots with high species richness and endemism (Myers et al. 2000), and both are of major economic importance for the global rice production. Their rice fields are found in lowlands and uplands, and can be grouped into irrigated and rainfed environments. The rice plants are either transplanted or directly seeded onto the fields (FAO 2000; GRiSP 2013).

Vietnam is the easternmost country on the Indochinese Peninsula. It is bounded by the Eastern Sea (South China Sea) in the east and by the Gulf of Thailand in the south and southwest, and shares its land borders with China to the north, and with Cambodia and Laos to the west. Most Vietnamese live in the two rice-growing deltas: the Red River Delta with the capital city Hanoi in the north, and the Mekong River Delta with the most populous city Ho Chi Minh City in the south. The most rice is produced in the Mekong River Delta, where 2–3 crops can be grown each year, although triple-cropped rice fields have nearly doubled in area between 2000 and 2010 (Kontgis et al. 2015). The total area of rice cultivation in Vietnam added up to 7.5 million ha in 2019 (FAO 2020). Rice is still the staple food in Vietnam, although its consumption has begun to decline with rising income in recent years (GRiSP 2013). In 2018, per capita consumption of rice (and products) totaled 205.5 kg per year (FAO 2020). Rice production hardly increased until the 1970s because the positive effects of the ‘Green

Revolution' were delayed by the Vietnam War, but growth rates of rice production in the 1980s and 1990s greatly surpassed those of all other Asian countries (Tran & Kajisa 2006). The country became a major rice exporter in the 1990s as a result of the decollectivization policies that were pursued since 1981 (Pingali & Xuan 1992). Total annual production quantities continually increased from 25 million tonnes in 1995 to 43.5 million tonnes in 2019, and today, Vietnam is the world's fifth-largest rice-producing country and second-largest rice-exporting country (GRiSP 2013; FAO 2020).

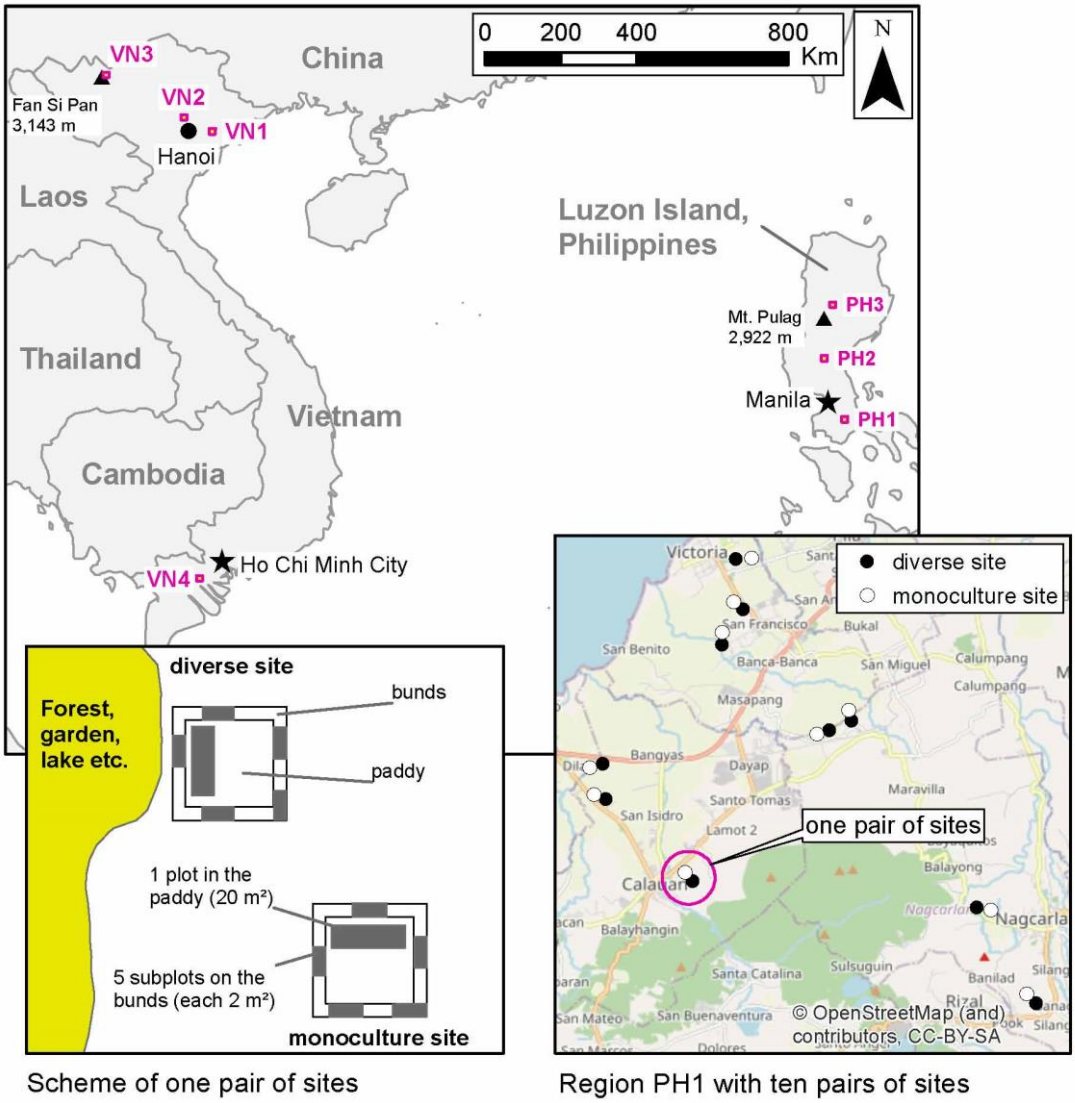

Fig. 1.7: Location of the seven study areas in Vietnam (VN1–4) and the Philippines (PH1–3). The lower right map shows the regional level, exemplified by PH1, comprising ten pairs of sites. The paired study design with diverse and monoculture sample sites on the landscape level is indicated on the lower left map.

The Philippines is an archipelago of about 7,641 islands in the western Pacific Ocean, separated from Vietnam by the Eastern Sea. It can be divided into three main

geographical divisions: Luzon, Visayas, and Mindanao. Most rice is produced in the central plain of the main island Luzon, popularly known as the country's rice bowl. Rice is also the staple food, but in contrast to Vietnam, rice consumption per capita continues to rise over time like in many other middle- to low-income Asian countries (GRiSP 2013). In 2018, per capita consumption of rice (and products) in the Philippines totaled 176.5 kg per year (FAO 2020). Rice production in the Philippines was profoundly changed with the establishment of the International Rice Research Institute (IRRI) in 1960 and its subsequent release of modern high-yielding rice varieties, such as the famous 'IR8' in 1966, which required the use of fertilizers and pesticides but produced substantially higher yields than traditional cultivars (Estudillo & Otsuka 2006). The breeding of new high-yielding varieties was one of the major improvements of the 'Green Revolution' for rice production in Asia and worldwide. But despite continuous efforts since the 1960s to achieve food security and rice self-sufficiency, the Philippines have nearly consistently imported rice in the last century (except during a short period in the 1980s) (Dawe 2013). Today, the Philippines is the world's eighth-largest rice-producing country, with 18.8 million tonnes of paddy rice produced in 2019 (FAO 2020). The area under rice cultivation has expanded from nearly 3.8 million ha in 1995 to 4.7 million ha in 2019, and more than two-thirds (69%) of this area are irrigated (GRiSP 2013; FAO 2020).

1.5. General methodology

1.5.1. Study area

We surveyed four study regions in Vietnam (VN1–4) and three in the Philippines (PH1–3), each covering 15 × 15 km (Fig. 1.7, Table 1.1).

The four Vietnamese study regions range from 10.40° to 22.41° N, from 103.84° to 106.44° E, and from sea level to 1,390 m a.s.l. They are located along the Red River in the northern provinces of Hai Duong (VN1), Vinh Phuc (VN2) and Lao Cai (VN3), and in the Mekong Delta in the southern province Tien Giang (VN4). The tropical to subtropical monsoon climate has a wet season from May to September dominated by southeasterly winds and a dry season caused by northeasterly winds between October and April. The southern Mekong Delta is characterized by warm-humid conditions all year round whereas temperatures in the subtropical north are cooler during the dry

season. Less warm summers and cool winters are typical in the northwestern mountains, although the local climate varies considerably. Mean annual temperatures range from 16 °C (Lao Cai) to 28 °C (Tien Giang), where mean annual precipitation differs between 2,500 mm and 1,500 mm, respectively (Rivas-Martinez & Rivas-Saenz 1996–2009; Sterling et al. 2008; Vân 2016).

Table 1.1: Southeast Asian study regions and important corresponding attributes related to geography, climate, management and sampling design. Land use intensity and structural diversity classes by Settele et al. (2013).

Country code	PH			VN				Total
Study region ID	PH1	PH2	PH3	VN1	VN2	VN3	VN4	
Province	Laguna	Nueva Ecija	Ifugao	Hai Duong	Vinh Phuc	Lao Cai	Tien Giang	-
High-/ Lowland	low	low	high	low	low	high	low	-
Latitude range (WGS84,°)	14.11 - 14.23	15.51 - 15.75	16.86 - 16.93	20.94 - 21.09	21.30 - 21.37	22.30 - 22.41	10.37 - 10.44	10.37 - 22.41
Longitude range (WGS84,°)	121.30 - 121.41	120.84 - 121.02	121.05 - 121.14	106.35 - 106.44	105.70 - 105.74	103.84 - 103.91	106.06 - 106.13	103.84 - 121.41
Land use intensity	medium - high	medium - high	low	medium - high	low - medium	low	high	low - high
Landscape heterogeneity	medium	low - medium	high	low - medium	medium	high	low - medium	low - high
Elevation range of study sites (m)	7 - 291	24 - 80	760 - 1182	0 - 13	3 - 78	725 - 1390	3 - 10	0 - 1390
Mean annual temperature range (°C)	26.4 - 27.6	26.7 - 27.1	17.6 - 22.1	23.9 - 24.2	24.4 - 24.9	17.6 - 22.0	28.1	17.6 - 28.1
Number of pairs of sites	10	18	9	10	10	5	5	67
Number of plots (paddy/bunds)	20/20	34/36	12/18	20/20	20/20	10/10	6/10	122/134

The three Philippine study regions range from 14.11° to 16.93° N, from 120.84° to 121.41° E, and from sea level to 1,095 m a.s.l. They are located on Luzon Island in the provinces of Laguna (PH1), Nueva Ecija (PH2) and Ifugao (PH3). The tropical climate is characterized by the southwest monsoon causing a wet season from May to October, and the northeast monsoon bringing the dry season between November and April. Local climates have relatively constant temperatures throughout the year, but vary in rainfall seasonality. Mean annual temperatures range from 19 °C in the mountains of Ifugao to 28 °C in the lowlands. Mean annual precipitation varies between 1,800 mm (Nueva

Ecija) and 3,700 mm (Ifugao). Tropical cyclones occur frequently between July and November (Coronas 1920; CRU et al. 2008; GRiSP 2013).

All seven study regions are also varied in landscape heterogeneity and land use intensity (Table 1.1). VN1, VN4 and PH2 are plain and rather monotone lowland regions with mostly high-intensity farming. Lowland regions VN2 and PH1 have a slightly more heterogeneous, hilly landscape and show rather medium land use intensity, although rice farming in PH1 is generally more intensive than in VN2. VN3 and PH3 are characterized by traditional low-input rice cultivation on rice terraces in heterogeneous mountain landscapes between 725 m and 1,390 m a.s.l.

1.5.2. Experimental design

A paired study design was employed, with pairs (landscape level) of study sites (plot level) in each region (regional level), to detect scale-dependent effects of abiotic conditions and surrounding landscape on the vegetation (details in Fig. 1.7, Table 1.1 and chapter 4.2.1). Each pair of sites comprised one monoculture site that was entirely surrounded by rice fields, and one structurally more diverse site that shared at least one border with one or more non-paddy habitats (e.g. agroforests or gardens) resulting in "diverse" surroundings (and representing an enhanced habitat diversity) (Fig. 1.7).

1.5.3. Data collection

This section provides a general overview of the data collection and more detailed descriptions follow in chapters 2–4. Field data were collected during wet and dry seasons between 2012 and 2015. In each study region, we established representative rectangular sampling plots in paddies (20 m²) and bunds (10 m²). Vascular plant species were recorded with their cover/abundance values using the nine-class Braun-Blanquet scale (Reichelt & Wilmanns 1973). Soil samples were collected and later analyzed in laboratories of Göttingen University and the Helmholtz Centre for Environmental Research – UFZ to assess electrical conductivity (EC), soil pH, and contents of C_{org}, N_{total} and humus at each plot. Soil texture, moisture, and rock fragments were determined in field through visible characteristics. Additionally, we documented plot size, a short description of the study site (including habitat type and Plot-ID), cover and maximum height of herbs, crop, and plants in total, crop stage, method of crop establishment (transplanting vs. direct seeding), and environmental variables

(geographic coordinates, exposition, slope, and altitude). Further, farmers of the surveyed rice fields were interviewed using standardized questionnaires on timing and practice of weed control, the number of crop cycles per year and the method of crop establishment. The data sheets used for the vegetation survey and the interviews are provided in Appendices B.1 and B.2, respectively. Additionally, the Potsdam Institute for Climate Impact Research supplied monthly mean temperatures from the years 2001 to 2006.

A number of complementary works were used for plant identification: Harada et al. 1987, 1993; Soerjani et al. 1987; Pancho & Obien 1995; Cook 1996; Ho 1999, 2000, 2003; Nguyen 2002; Le 2007; Nguyen & Nguyen 2007; eFloras 2008. Nomenclature of taxa follows The Plant List (2013). The names of syntaxa follow Mucina et al. (2016), complemented by Nowak et al. (2015) for the *Oryzetea sativae* and Landolt (1999) for the *Lemnetea*. Plant life form classes mainly follow Ellenberg & Mueller-Dombois (1967) (Appendix A.1).

1.5.4. Data analysis

In this thesis, I used different methods of multivariate analyses to investigate the diversity and composition of the rice weed vegetation. Common to all following studies is the separate treatment of the data of bunds and paddies. Further, cultivated species are listed in these studies, but were generally disregarded during analyses of plant species diversity and composition.

In chapter 2 and 3, classifications and ordinations were applied to differentiate the main vascular plant communities in bunds and paddies, and identify the environmental drivers that shape them. In both habitat types, hierarchical UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis was applied. Weed communities in paddies were further edited manually. Afterwards, synoptic tables were prepared and differential taxa were determined with the algorithm of Tsiripidis et al. (2009). Plant species and communities were assigned to higher-rank syntaxa based on literature.

In chapter 4, linear mixed-effects models (LME) with a Gaussian error distribution and generalized linear mixed-effects models (GLMM) with a Poisson error distribution were developed to identify predictor variables with highest explanatory value and significant effect ($p < 0.05$) on different indices of plant species diversity, i.e. species richness,

Shannon diversity, and the number of insect-pollinated species. We included information on the geographic location of sites into the random term of the models to account for the non-independence of sites within landscapes (or pairs, respectively) and regions. Further, the compositional dissimilarity between sampling sites, and between regions, was calculated based on the Bray-Curtis coefficient (Bray & Curtis 1957) to quantify and visualize the species turnover in the study area. Detrended correspondence analysis (DCA) was performed on the species data to visualize differences in the species composition between paddies and their bunds, and between regions.

1.6. Research objectives, motivation and chapter outline

This thesis was conducted within the framework of the interdisciplinary research project LEGATO (**L**and-use intensity and **E**cological en**G**ineering – **A**ssessment **T**ools for risks and **O**pportunities in irrigated rice-based production systems; Settele et al. 2018). Assessing the biodiversity in rice ecosystems was one of the focal issues of the project, which aimed at advancing long-term sustainable development of irrigated rice landscapes against risks arising from future climate and land use change (Settele et al. 2015). Biodiversity generally enhances the resilience of agroecosystems against disturbances and provides other valuable services, e.g. pollination and biocontrol (Fischer et al. 2006). Particularly the floristic composition and distribution of rice weeds often serves as a key indicator of field conditions, but the knowledge of the rice weed communities is still inadequate (Moody & Drost 1983), especially in the study area. A more comprehensive understanding of the relationships between floristic communities, environmental conditions, surrounding landscape, and agricultural management is a prerequisite to conserve the valuable plant diversity in rice landscapes and develop effective tools of ecological engineering. In this thesis, I studied the vascular plant communities in irrigated rice ecosystems of Vietnam and the Philippines. The main aims of this research were (1) to reveal the diversity and composition of rice weed communities of major Southeast Asian centers of rice cultivation, (2) to compare the diversity of their rice weed flora among rice fields within and between regions, and between habitat types, and (3) to disentangle the effects of environmental variables, surrounding landscape, agricultural management and phytogeographic patterns on the composition, distribution and diversity of rice weeds.

Chapter 2 and 3 are both devoted to the abundance, distribution and composition of vascular plant communities occurring in the local rice ecosystems, but focus on different habitat types. The study in **chapter 2** is focused on the weeds associated with rice in paddies, whereas the study in **chapter 3** deals with the vegetation on adjacent bunds. In both studies, classical methods of community ecology are applied. First, the main rice weed communities are differentiated with hierarchical cluster analyses and presented in synoptic tables to show their differential taxa. In a second step, ordination methods are performed to visualize differences in plant community composition along gradients of environmental and other variables, i.e. geographic location, elevation, temperature, soil properties, landscape heterogeneity, season, number of crops/year, crop cover and height, herb cover and height, and species diversity. Further, a detailed description of the floristic diversity is presented. Following questions are addressed:

Which plant species can be found in the rice fields of selected areas in Vietnam and the Philippines? Which plant communities occur and what are the prevailing life forms? What are the main environmental drivers and phytogeographic patterns that shape these communities? How does the bund vegetation in terms of species diversity and composition compare to that of adjacent paddies?

The study in **chapter 4** is focused on two different aspects of the vascular plant species diversity in the study area, namely the field-level weed diversity (alpha diversity) and the compositional heterogeneity of different sites (species turnover or beta diversity). An explorative modeling approach is used to identify major drivers of rice weed (alpha) diversity and to visualize their effects. Different methods of quantitative community ecology are applied to visualize the species turnover in the study area on different scales. Aim of this study was to answer the following questions:

What are the abiotic conditions and surrounding landscapes in the local paddy rice ecosystems and what is their relative importance for vascular plants? How and to which extent do plant diversity and composition differ within a region, between the paddies and their bunds, and across regions?

In the final **chapter 5**, the key findings of the three studies are summarized and the differences and similarities of bunds and paddies are highlighted. The chapter concludes with a discussion of the major findings, and indicates remaining issues and future

implications for the conservation of biodiversity and the sustainable management of rice ecosystems.

Chapter 2:

Plant diversity and community composition of rice agroecosystems in Vietnam and the Philippines

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Abstract

Aims: The knowledge of rice weed communities, their diversity, composition, dynamics and distribution is still inadequate. We present information on the plant diversity of rice fields in major Southeast Asian centers of rice cultivation, the prevailing life forms, the plant communities, the main environmental drivers, and phytogeographic patterns that shape these communities. **Study area:** Seven different regions of Vietnam and the Philippines, including lowland and mountain areas (0–1390 m a.s.l.). **Methods:** Altogether 115 vegetation relevés using the Braun-Blanquet method were recorded during wet and dry seasons between 2013 and 2015. Soil samples were collected and farmers of surveyed rice fields were interviewed. Vegetation surveys were designed to detect possible effects of soil properties, climate, altitude, geographic location, landscape heterogeneity, seasonality, management and intensity of cultivation, and structural parameters on the paddy vegetation. Hierarchical cluster analysis UPGMA was applied and NMDS ordinations were performed to visualize differences in plant community composition along the different gradients. **Results:** We found 113 vascular plant species, with annual hydrophytes and therophytes being the prevailing life forms. Sixty of the recorded species appear to be globally rare. We revealed four clusters of plant communities which are explained mainly by soil acidity, crop height and temperature: *Paspalum distichum-Hydrolea zeylanica* community, *Echinochloa crus-galli* community, *Rotala indica-Monochoria vaginalis* community and *Fimbristylis littoralis-Leptochloa chinensis* community. The two latter communities were further classified into regional subunits. **Conclusions:** We conclude that the composition of weed communities provides valuable information on environmental and biogeographical conditions of the local rice landscapes, and that it is probably the most applicable and reliable indicator of management intensity.

2.1 Introduction

Rice is the staple food for more than half of the world's population and has fed more people longer than any other crop (GRiSP 2013). For 2015 the FAO forecasted a global rice production of 490.3 million tonnes (milled basis), of which Asia contributes by far the major part of 443.4 million tonnes (FAO 2016). Particularly in Southeast Asia, most countries are highly dependent on their rice yields to meet the increasing demands for food and economical security of a growing population. In Vietnam and the Philippines, rice consumption in 2013 totaled 144.6 kg and 119.4 kg per person per year, respectively. Southeast Asia's rice cultivation areas constitute 48.8 million ha in 2014, comprising 7.8 million ha in Vietnam and 4.7 million ha in the Philippines (FAO 2016; FAO 2020). Beside its economic relevance, rice cultivation is also deeply ingrained in the life and cultural habits of the local people (Pretty 2002; Tekken & Settele 2014).

The Asian rice agroecosystems faced enormous changes through intensification since the 'Green Revolution' in the 1960s (Bambaradeniya & Amerasinghe 2003). The input of chemical fertilizers and pesticides increased, and new technologies and high-yielding varieties were introduced. With more efficient technical and labor input, yields were maximized, hunger reduced, nutrition improved, and, it is said, natural ecosystems spared from conversion to agriculture (Tilman et al. 2002). The negative effects of these changes are degradation of soils and water resources, decreasing agrobiodiversity, increasing pest outbreaks, decreased health of people and animals, increasing commitments of farmers, and unstable yields (Tekken & Settele 2014).

More than 8,000 years of rice cultivation in Asia have created specifically adapted ecosystems (e.g. Bambaradeniya & Amerasinghe 2003; GRiSP 2013). The plant communities which co-evolved with their associated crop, are adapted to its phenology, its environment and related agri- and sociocultural practices. Several studies describe these ecosystems in detail, their biotic and abiotic factors, agricultural management, nutrient cycles, and biodiversity (e.g. De Datta 1981; FAO 2000; Bambaradeniya & Amerasinghe 2003; GRiSP 2013). In Vietnam and the Philippines, rice fields can be grouped into irrigated and rainfed, lowland and upland, and rice plants being either transplanted or directly seeded onto the fields (FAO 2000; GRiSP 2013).

The flora associated with rice cultivation, commonly referred to as 'rice weeds', is diverse and well adapted to its frequently disturbed habitat. Based on a literature review,

Moody (1989) listed more than 1,800 rice weed species for South and Southeast Asia alone. Rice weeds colonize mainly three different habitat types: the field proper (paddy), the bund (levee) and the ditch (water supply canal) (Barrett & Seaman 1980; Bambaradeniya & Amerasinghe 2003). Each of these habitats supports distinct weed communities.

Approaches to classify rice weed communities have been carried out since the 1950s in the Mediterranean (Bolòs & Masclans 1955; Tallon 1958; Piccoli & Gerdol 1981; Carretero 1988, 1989; Parras & Lorca 1993; García & Benzal 2009), Egypt (Turki & Sheded 2002), Japan (Miyawaki 1960), Korea (Kolbek et al. 1996; Kim & Nam 1998; Kim 2001), and recently in Tajikistan (Nowak et al. 2013), Java (Kumalasari 2014), Thailand (Nowak et al. 2015) and Nepal (Nowak et al. 2016). In other major centers of rice cultivation, however, such as Vietnam and the Philippines, the rice weed diversity at the community level, is as yet, almost unknown.

Several authors have pointed out that the knowledge of rice weed communities, their diversity, composition, dynamics and distribution is inadequate (e.g. Barrett & Seaman 1980; Moody & Drost 1983; Nowak et al. 2016). A more comprehensive understanding of the Southeast Asian rice agroecosystems and the underlying ecological processes is a prerequisite to maintaining their services and function.

In this paper, we focus on the abundance, distribution and composition of vascular plant communities associated with rice in Vietnam and the Philippines to answer the following questions: (1) Which plant species can be found in the rice fields of selected areas in Vietnam and the Philippines? (2) Which plant communities occur and what are the prevailing life forms? (3) What are the main environmental drivers and phytogeographic patterns that shape these communities?

2.2 Study area

Seven study regions were surveyed in Vietnam and the Philippines, each covering 15 km x 15 km (Fig. 1.7, Table 1.1). Detailed information on the local climate, geography, landscape heterogeneity, and land use intensity is given in chapter 1.5.1.

2.3 Methods

2.3.1 Data collection

A total of 115 vegetation relevés was recorded in representative rectangular plots of 20 m² in rice paddies during wet and dry seasons of 2013–2015. The seven study areas were represented by 6 to 33 relevés, each (Table 2.1). As part of the LEGATO project (Settele et al. 2015), the vegetation survey was designed to detect possible effects of landscape heterogeneity on the paddy vegetation (cf. Klotzbücher et al. 2015). Paddies were sampled preferentially according to the accessibility of rice fields and approachability of farmers during the sampling period. Vascular plant species were recorded with their cover/abundance values using the nine-class, Braun-Blanquet scale (Reichelt & Wilmanns 1973). Altitude and geographical coordinates of the plots were determined with a GPS (Garmin eTrex Vista® HCx) device.

Plant identification followed Harada et al. 1987, 1993; Soerjani et al. 1987; Pancho & Obien 1995; Cook 1996; Ho 1999, 2000, 2003; Nguyen 2002; Le 2007; Nguyen & Nguyen 2007; eFloras 2008). Voucher specimens of each species were collected and curated in the herbarium GOET (University of Göttingen). The floating waterplant *Lemna aequinoctialis* was always accompanied by *Lemna minor*. As separate cover-abundance estimation was not feasible, the species are treated as *Lemna aequinoctialis + minor*.

Plant life form classes follow Ellenberg & Mueller-Dombois (1967), except for hydrophytes which include partly submerged, amphibious plants (helophytes) (Appendix A.1). Some recorded species were assigned to several life forms, e.g. annual hydrophytes or species that occur either as annual or perennial plants depending on local conditions.

Mixed soil samples were collected (10–20 cm depth) from five locations in each paddy field and later analyzed in Göttingen University and the UFZ (Helmholtz Centre for Environmental Research – UFZ). Electrical conductivity (EC) was measured with a conductivity gauge of the type pH538 (WTW GmbH) in the supernatant suspension of a 1:2.5 soil:H_2O mixture, before assessing the soil pH with a pH meter of the type pH358 (Krannich GmbH & Co.KG). Contents of C_{org} and N_{total} were measured with the Dumas combustion method using a VARIO MAX (elementar), after which, humus content

Table 2.1: The vegetation on Southeast Asian rice fields was studied between 2013 and 2015. Study regions and important corresponding attributes related to geography, climate and management are listed. Additionally, the number of collected relevés, the number of recorded taxa and the percentage of recorded taxa from the total species pool assessed during the study are given for each region. Information on land use intensity and structural diversity is taken from Settele et al. (2013).

Country code	Study area ID	Province	High-/ Lowland	Latitude range (WGS84,°)	Longitude range (WGS84,°)	Land use intensity	Structural diversity	Elevation range of study sites (m)	Mean temperature range (°C)	Number of relevés	Number of taxa	Taxa (%)
PH	PH1	Laguna	low	14.1 - 14.2	121.3 - 121.4	medium - high	medium	7 - 291	26.4 - 27.6	18	51	46
	PH2	Nueva Ecija	low	15.5 - 15.7	120.8 - 121.0	medium - high	low - medium	24 - 80	26.7 - 27.1	33	27	24
	PH3	Ifugao	high	16.8 - 16.9	121.0 - 121.1	low	high	760 - 1095	18.8 - 22.1	9	41	37
VN	VN1	Hai Duong	low	20.9 - 21.0	106.3 - 106.4	medium - high	low - medium	0 - 13	23.9 -24.2	20	38	34
	VN2	Vinh Phuc	low	21.3	105.7	low - medium	medium	3 - 78	24.5 - 24.9	19	44	39
	VN3	Lao Cai	high	22.3 - 22.4	103.8 - 103.9	low	high	725 - 1390	17.6 - 22.0	10	44	39
	VN4	Tien Giang	low	10.4	106.0 - 106.1	high	low - medium	3 - 10	28.0 - 28.1	6	6	5
Total	-	-	high + low	10.4 -22.4	103.8 - 121.4	low - high	low - high	0 - 1390	17.6 - 28.1	115	113	100

was estimated (C_{org} × 1.725). Texture was evaluated on a moist sample of fine earth and through visible characteristics (FAO 2006).

Four categories of soil moisture with increasing water content were distinguished: 1 − moist but solid soil; 2 − wet and soft soil; 3 − very wet and muddy soil with interspersed puddles; 4 − flooded soil completely covered by water.

Farmers of the surveyed rice fields were interviewed using standardized questionnaires on timing and practice of weed control, the number of crop cycles per year and the method of crop establishment.

Monthly mean temperatures from the years 2001−2006 were supplied by the Potsdam Institute for Climate Impact Research and are based on a time-series data set (CRU TS 3.0) provided by CRU et al. (2008).

2.3.2 Data analyses

Cover-abundance values were converted to percentages (r = 0.1, + = 0.5, 1 = 2.5, 2m = 2.5, 2a = 10, 2b = 20.5, 3 = 37.5, 4 = 62.5, 5 = 87.5) (Dierschke 1994). The cultivated species *Oryza sativa* L. as well as singletons and doubletons were eliminated from the data set before excluding plots without weeds. The species data of the remaining 102 relevés were log transformed and hierarchical cluster analysis UPGMA (Unweighted Pair Group Method with Arithmetic Mean) based on Bray-Curtis dissimilarity applied. A synoptic table was prepared using JUICE 7.0 (Tichý 2002). Differential taxa were determined with the algorithm of Tsiripidis et al. (2009). Further differentiation based on species within UPGMA clusters was carried out manually and is displayed in the full relevé tables (Appendices A.2−4).

Nonmetric multidimensional scaling (NMDS), commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987), was performed to visualize differences in plant community composition along gradients of environmental and other variables, i.e. elevation, temperature, soil properties (moisture, pH, EC, C_{org}/N_{total}, humus content), landscape heterogeneity (high vs. low), season (dry vs. wet), number of crops/year, crop cover and height, herb cover and height, and species diversity. Additionally, a Wisconsin double standardization and a square root transformation of the original cover-abundances were performed as they improved the ordination results. NMDS ordinations (based on Bray-Curtis dissimilarities and random

starting configurations) were optimized for two dimensions after examination of a scree stress plot and by visual inspection and comparison of resulting ordination graphs. The strength of the ordination was assessed using the final stress. Environmental variables were fitted *a posteriori* to the ordination using 999 permutations. The parameter "elevation" was excluded due to strong negative correlation with "mean annual temperature". Insignificant variables ($p > 0.05$) were also excluded. Information on weed control is summarized in Table 2.2.

Table 2.2: Farmers of the surveyed rice fields were interviewed on timing and practice of weed control. The number of rice fields that are subject to the applied methods varies between clusters, countries and altitudinal levels.

		Herbicide use				Handweeding					Harrowing			Grazing		N° of plots
	Times/season	3	2	1	0	4	3	2	1	0	2	1	0	1	0	
Cluster	C1	4	4	17	7	3	8	7	12	2	10	10	12	8	23	33
	C2	0	0	9	1	1	2	2	3	2	1	0	9	1	8	29
	C3	0	1	1	0	0	0	0	0	2	0	0	2	0	2	5
	C4	0	2	24	7	4	10	7	6	8	0	10	25	1	34	35
	empty plots	0	1	5	4	0	1	3	2	3	0	5	4	0	9	13
High-/ Lowland	high	0	0	3	14	4	0	10	5	0	0	19	0	0	19	19
	low	4	8	53	5	4	21	9	18	17	11	6	52	10	57	96
Country	PH	4	1	18	11	4	3	7	12	7	11	9	13	5	26	60
	VN	0	7	38	8	0	18	12	11	10	0	16	39	5	50	55

Species richness estimates in Fig. 2.1a are based on incidences of species in sample sites and were calculated with the nonparametric Jack 2 (second-order jackknife) estimator (Burnham & Overton 1979):

$$S_P = S_{obs} + a1\frac{(2N-3)}{N} - a2\frac{(N-2)^2}{N(N-1)}$$

, with S_p being the extrapolated richness in a pool, S_{obs} being the observed number of species in the collection, *a1* and *a2* being the number of species occurring only in one or only in two sites in the collection, and *N* being the number of sites in the collection.

All multivariate analyses of the data were performed with the packages *vegan* (Oksanen et al. 2019) and *cluster* (Maechler et al. 2015) of the R software (version 3.2.3, R Core Team 2018). Species richness estimators are included in the *vegan* package. The names of syntaxa follow Mucina et al. (2016), complemented by Nowak et al. (2015) for the

Oryzetea sativae and Landolt (1999) for the *Lemnetea*. Species assignation to higher-rank syntaxa (Appendices A.2−4) is based on literature (Bolòs & Masclans 1955; Miyawaki 1960; Landolt 1999; Nowak et al. 2015).

2.4 Results

2.4.1 Floristic diversity

A total of 113 different plant species was recorded in rice fields in the study areas, belonging to 77 genera and 38 families (Table 2.1, Appendix A.5). Most taxa belong to the *Poaceae* (22), followed by *Cyperaceae* (16) and *Lythraceae* (10). The most common species found in paddies were *Paspalum distichum* (37 relevés), *Fimbristylis littoralis* (33), *Hydrolea zeylanica* (32), *Leptochloa chinensis* (30), *Alternanthera sessilis* (29), *Monochoria vaginalis* (28), *Ludwigia hyssopifolia* (26), *Lindernia antipoda* (26), *Echinochloa oryzoides* (24) and *Rotala indica* (23). These are all character species of the phytosociological class *Oryzetea sativae*, but genera of many other classes were interspersed in the rice fields, e.g. the free floating pleustons of the *Lemnetea* (*Azolla, Eichhornia, Lemna, Pistia* and *Spirodela*) or submerged aquatic plants of the *Potametea* (*Potamogeton*) and *Charetea fragilis* (*Characeae* spec.), further therophytes of the *Bidentetea tripartitae* (*Bidens, Persicaria, Eclipta*) and *Stellarietea mediae* (*Digitaria*, *Eragrostis*, *Oxalis* etc.), and perennial, mostly graminoid, species of the *Phragmito-Magno-Caricetea* (*Eleocharis*, *Leersia*, *Oenanthe* etc.). Characteristic highland species are *Cuphea carthagenensis*, *Cyperus pilosus*, *Persicaria minor*, *Sagittaria trifolia* and *Schoenoplectiella juncoides*, whereas *Ammannia baccifera*, *Hydrolea zeylanica* and *Sphenoclea zeylanica* were only encountered in lowland paddies (Table 2.3). All diagnostic species occur in both countries (eFloras 2008; IUCN 2015; Roskov et al. 2015), with few of them encountered in this study in the paddies of only one country, e.g. *Rotala indica* only in Vietnam, *Ammannia baccifera* in the Philippines (Table 2.3).

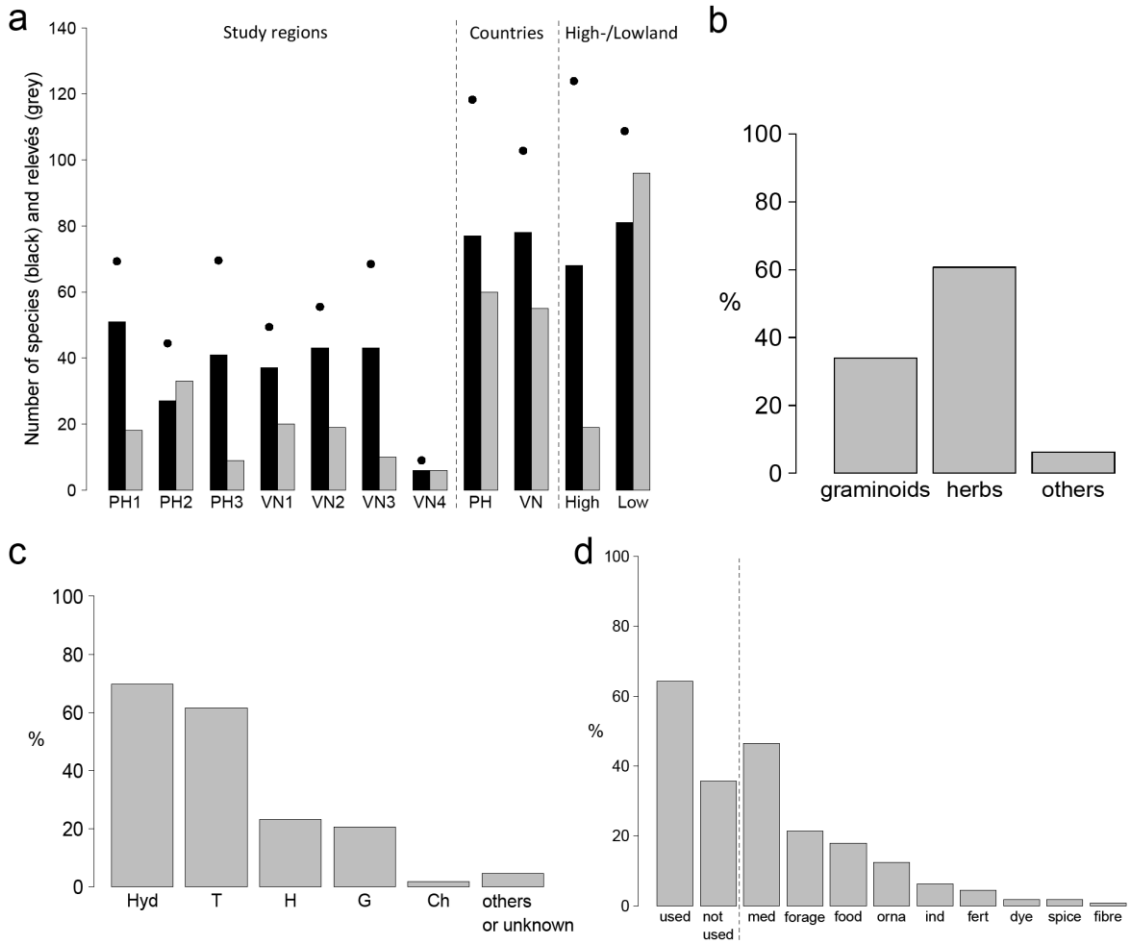

Fig. 2.1: The floristic diversity and composition in Vietnamese and Philippine rice fields was investigated from 2013 to 2015: (a) Numbers of species (black) and relevés (grey) in the different study regions, countries and altitudinal levels. Black dots represent estimated numbers of species. Percentages of (b) graminoids and herbs and (c) plant life forms occurring in rice fields (Hyd = hydrophytes, T = therophytes, H = hemicryptophytes, G = geophytes, Ch = chamaephytes). (d) Percentages of useful plants encountered in the studied rice fields (med = medicine, orna = ornamental, ind = industrial resource, fert = fertilizer), multiple use possible (IUCN 2015; eFloras 2008).

Species richness in the rice fields was generally low (mean: 7.7, standard deviation (SD): 5.8) and ranged between 0 and 29 weed species per sample plot. Fifty-one species occurred with less than 2% constancy. The total number of recorded species was roughly the same for the two countries (Fig. 2.1a), as was the mean number of species recorded per paddy (Two Sample t-Test, $t_{113} = -0.90$, $p = 0.369$). Species richness and sampling effort was lowest in region VN4, whereas the area with most species was PH1 while most relevés were recorded in PH2. Although the number of relevés in the two highland regions was considerably less than in the five lowland regions, the total amount of recorded taxa was only slightly higher in the lowlands. The mean number of recorded species was not significantly different between the two altitudinal levels (Welch Two Sample t-Test, $t_{112} = -0.91$, $p = 0.3659$).

Table 2.3: Synoptic table showing common species in Southeast Asian rice fields with their constancies (%) in each country and altitudinal level. Differential taxa (darkgrey bold = positively differentiating, lightgrey italic = negatively differentiating, grey bold italic= positive-negatively differentiating) were identified with the algorithm of Tsiripidis et al. (2009).

Country	**PH**		**VN**	
High-/Lowland	**low**	**high**	**low**	**high**
Number of relevés	46	5	41	10
Taxon				
Hydrolea zeylanica	**50**	*0*	**22**	*0*
Persicaria minor	*0*	**60**	*2*	**70**
Schoenoplectiella juncoides	*0*	**60**	*7*	**40**
Monochoria vaginalis	*17*	**60**	27	**60**
Ageratum conyzoides	*0*	**40**	*0*	**20**
Ammannia baccifera	**28**	*0*	*0*	*0*
Ischaemum rugosum	**20**	*0*	*0*	*0*
Echinochloa colona	**20**	*0*	7	*0*
Sphenoclea zeylanica	**39**	*0*	10	*0*
Fimbristylis littoralis	*35*	**100**	*24*	*20*
Azolla pinnata	*4*	**80**	*15*	*10*
Cyperus difformis	*22*	**80**	*10*	*20*
Cuphea carthagenensis	*0*	**60**	*0*	*0*
Cyperus pilosus	*0*	**60**	*0*	*0*
Ludwigia octovalvis	*20*	**60**	*7*	*0*
Cardamine hirsuta	*0*	**40**	*0*	*10*
Kyllinga brevifolia	*9*	**40**	*0*	*10*
Eclipta prostrata	22	**60**	*17*	30
Lindernia antipoda	22	**60**	27	*20*
Cyperus iria	*7*	**40**	12	*0*
Lindernia anagallis	*0*	**40**	15	*0*
Cyperus haspan	*0*	**40**	7	20
Spirodela polyrrhiza	*0*	*0*	**24**	*0*
Pistia stratiotes	*0*	*0*	**22**	*0*
Alternanthera philoxeroides	*0*	*0*	**20**	*0*
Rotala indica	*0*	*0*	***34***	**90**
Sagittaria trifolia	*0*	*0*	*0*	**70**
Commelina diffusa	*9*	*0*	12	**40**
Echinochloa crus-galli	15	*0*	24	**50**
Lemna aequinoctialis + minor	*0*	*0*	**37**	**30**
Ludwigia prostrata	*0*	*0*	**22**	**30**
Ludwigia hyssopifolia	**26**	**60**	**27**	*0*
Alternanthera sessilis	**33**	**40**	**29**	*0*
Leptochloa chinensis	**26**	**20**	**41**	*0*
Paspalum distichum	**54**	**20**	**27**	*0*
Echinochloa oryzoides	*4*	**60**	**44**	*10*

The majority of species encountered were non-graminoid herbs (ca. 60%), with graminoids contributing nearly 40% (Fig. 2.1b). Hydrophytes (70%) were most numerous, closely followed by therophytes (63%), both categories being mostly represented by annuals (Fig. 2.1c). Perennials (hemicryptophytes and geophytes) occurred only in low percentages (23% and 20%, respectively). Other life forms such as woody lianas, chamaephytes and phanerophytes did not occur other than in the seedling stage.

Of the recorded species, 72 are used as food, spice, forage, medicine, fiber, ornamental plant or as an industrial resource, with some species being useful for multiple purposes (Fig. 2.1d, Appendix A.5) (eFloras 2008; IUCN 2015). The relevés contained a total of 60 red listed species, albeit mostly of "least concern" (IUCN 2015).

2.4.2 Classification of relevés and determination of diagnostic species

UPGMA classification of the paddy vegetation revealed four clusters (see dendrogram in Appendix A.6). The differential species of the clusters and species occurring more than two times are listed in a synoptic table (Table 2.4). The differentiation of the vegetation seems to be mainly related to the acidity of the soils, and also to crop height, indicating distinct stages of the cultivation cycle (Table 2.5). Elevation and mean annual temperature also have a major influence, as clusters C2 and C3 are restricted to the lowlands. Other important features of the clusters become apparent through differences in nutrient availability (EC levels and humus contents), species richness, seasonality, intensity of cultivation (crops/year and crop cover) and geographical distribution. The first division separates the species-poor clusters C2 and C3 from the clusters C1 and C4: the latter two include a much broader range of species. *Alternanthera sessilis*, *Leptochloa chinensis* and *Lindernia antipoda* positively differentiate both C1 and C4, and underline the close relation between the two clusters. Both clusters can be further differentiated into subunits with a strong regional character (Appendices A.2 and A.4). All diagnostic species belong to the *Oryzetea sativae*, except for *Commelina diffusa* which is a widespread tropical weed found in various agroecosystems, and *Lemna aequinoctialis*, *L. minor*, *Spirodela polyrrhiza*, *Pistia stratiotes* and *Azolla pinnata*, which represent the *Lemnetea*.

Table 2.4: Synoptic table showing the differential species in Southeast Asian rice fields with their constancies (%) in the different clusters. Differential taxa (darkgrey bold = positively differentiating, lightgrey italic = negatively differentiating) were identified with the algorithm of Tsiripidis et al. (2009).

ClusterID	C1	C4	C2	C3
Number of relevés	33	35	29	5
Positive differential species of C1				
Fimbristylis littoralis	**73**	*17*	*10*	*0*
Cyperus difformis	**45**	11	*0*	20
Ludwigia hyssopifolia	**42**	26	10	*0*
Eclipta prostrata	**39**	23	7	*0*
Ammannia baccifera	**33**	*0*	7	*0*
Leersia hexandra	**27**	17	*0*	*0*
Ischaemum rugosum	**21**	*0*	7	*0*
Echinochloa colona	**21**	6	10	*0*
Positive differential species of C4				
Rotala indica	*6*	**57**	*3*	*0*
Lemna aequinoctialis + minor	*0*	**51**	*0*	*0*
Echinochloa oryzoides	21	**43**	7	*0*
Monochoria vaginalis	33	**40**	*7*	20
Spirodela polyrrhiza	*0*	**29**	*0*	*0*
Pistia stratiotes	*0*	**26**	*0*	*0*
Ludwigia prostrata	*3*	**26**	7	*0*
Sagittaria trifolia	*0*	**20**	*0*	*0*
Azolla pinnata	18	**20**	*0*	*0*
Commelina diffusa	12	**20**	7	*0*
Positive differential species of C2				
Paspalum distichum	*18*	*20*	**76**	40
Hydrolea zeylanica	27	*14*	**55**	40
Positive differential species of C3				
Echinochloa crus-galli	*15*	*31*	*3*	**100**
Differential species with at least 30% constancy				
Leptochloa chinensis	**58**	**29**	*3*	*0*
Lindernia antipoda	**45**	**31**	*0*	*0*
Alternanthera sessilis	**45**	**26**	17	*0*
Sphenoclea zeylanica	**27**	*6*	**38**	*0*
Ludwigia octovalvis	**33**	*0*	10	**20**
Species with more than two occurrences				
Ipomoea aquatica	6	3	3	20
Cyperus iria	18	9	3	0
Cyperus haspan	9	9	3	0
Lindernia anagallis	9	11	3	0
Panicum repens	18	9	3	0
Alternanthera philoxeroides	3	17	3	0
Rotala rosea	6	3	3	0
Oldenlandia corymbosa	3	3	3	0
Lindernia procumbens	9	17	0	0
Persicaria minor	15	17	0	0
Schoenoplectiella juncoides	12	17	0	0
Kyllinga brevifolia	18	0	3	0
Rotala ramosior	15	3	0	0
Phyllanthus urinaria	12	3	0	0
Ageratum conyzoides	9	3	0	0
Eriocaulon cinereum	3	0	10	0
Marsilea minuta	6	11	0	0
Rotala rotundifolia	3	6	0	0
Ammannia multiflora	6	6	0	0
Isachne globosa	6	9	0	0
Ludwigia adscendens	6	6	0	0
Paspalum conjugatum	6	0	7	0
Drymaria cordata	6	3	0	0
Eleusine indica	18	0	0	0
Rorippa indica	12	0	0	0
Aeschynomene indica	12	0	0	0
Cuphea carthagenensis	9	0	0	0
Bacopa rotundifolia	9	0	0	0
Mikania cordata	9	0	0	0
Cyperus pilosus	9	0	0	0
Basilicum polystachyon	9	0	0	0
Cardamine hirsuta	9	0	0	0
Ceratopteris thalictroides	0	9	0	0
Sphaeranthus africanus	9	0	0	0

Table 2.5: The vegetation survey was designed to detect possible effects of environmental and other variables on the Southeast Asian paddy vegetation. The important parameters characterizing the occurring vegetation clusters are summarized. "Mean annual temperature", "pH", "EC", "Humus content", "Number of crops", "Crop cover", "Crop height", "Herb height" and "Number of species" are represented as means ± standard deviation.

Cluster ID	C1a	C1b	C1c	C1	C2	C3	C4	C4a	C4b	C4c
Min. elevation (m)	0	7	18	0	0	41	0	725	0	0
Max. elevation (m)	823	277	1258	1285	186	80	1390	1390	36	26
Median elevation (m)	5	20	837	19	52	54	10	1224	12	0
Mean annual temperature	25.8 ± 2.1	27.4 ± 0.3	20.7 ± 2.5	25.6 ± 2.9	26.6 ± 0.9	26.9 ± 0.1	23.3 ± 2.4	19.6 ± 1.5	24.7 ± 0.3	24.3 ± 0.2
pH	4.62 ± 0.81	6.24 ± 0.60	5.49 ± 0.35	5.54 ± 1.00	6.10 ± 0.74	6.08 ± 0.67	5.50 ± 0.75	5.34 ± 0.27	5.45 ± 0.73	5.77 ± 0.80
EC (µS cm^{-1})	981 ± 1110	337 ± 201	176 ± 114	528 ± 730	132 ± 80	131 ± 89	259 ± 385	79 ± 46	168 ± 105	299 ± 234
Humus content (%)	3.9 ± 1.5	4.1 ± 1.76	4.3 ± 2.3	4.1 ± 1.7	2.1 ± 0.9	2.3 ± 0.8	2.5 ± 1.2	2.9 ± 0.8	2.2 ± 1.1	2.1 ± 0.7
Number of crops (yr^{-1})	2.3 ± 0.6	2.0	1.2 ± 0.4	1.9 ± 0.6	2	2.4 ± 0.5	1.8 ± 0.5	1.0	2.0	2.0
Crop cover (%)	65 ± 16	59 ± 17	53 ± 16	60 ± 16	59 ± 25	82 ± 12	75 ± 15	89 ± 10	65 ± 13	71 ± 10
Crop height (cm)	102 ± 23	82 ± 16	102 ± 25	92 ± 22	60 ± 30	78 ± 31	114 ± 16	107 ± 17	116 ± 13	120 ± 13
Herb height (cm)	77 ± 33	61 ± 19	103 ± 42	74 ± 32	24 ± 30	93 ± 39	89 ± 30	80 ± 46	102 ± 15	84 ± 24
Number of species	6 ± 3	14 ± 4	20 ± 6	12 ± 7	4 ± 3	3 ± 2	9 ± 4	8 ± 3	10 ± 4	9 ± 5
Season (n° of relevés)	dry (5), wet	dry (16)	wet (6)	dry (21),	dry (24),	dry (5)	dry (1), wet	wet (9)	wet (10)	wet (15)
Herbs (%)	69.0	62.3	61.9	64.2	55.9	55.6	75.4	74.1	67.6	64.7
Graminoids (%)	31.0	37.7	38.1	35.8	44.1	44.4	24.6	25.9	32.4	35.3
Region (n° of relevés)	PH1 (1), PH3 (1), VN1 (2), VN2 (3), VN4 (4)	PH1 (15), PH2 (1)	PH3 (4), VN2 (1), VN3 (1)	PH1 (16), PH2 (1), PH3 (5), VN1 (2), VN2 (4), VN3 (1), VN4 (4)	PH1 (2), PH2 (22), VN1 (1), VN2 (4)	PH2 (5)	VN1 (14), VN2 (11), VN3 (9), VN4 (1)	VN3 (9)	VN1 (2), VN2 (8)	VN1 (12), VN2 (3)
Country (n° of relevés)	PH (2), VN (9)	PH (16)	PH (4), VN (2)	PH (22), VN (11)	PH (24), VN (5)	PH (5)	VN (35)	VN (9)	VN (10)	VN (15)
Soil texture	Silt loam - Heavy clay	Silt loam - Heavy clay	Clay loam - Silty clay	Silt loam - Heavy clay	Sandy loam - Heavy clay	Sandy loam - Silty clay loam	Sandy loam - Silty clay	Sandy loam - Silty clay	Sandy loam - Silty clay loam	Silty loam - Silty clay

2.4.3 Indirect gradient analysis

Relationships between the plant community composition and observed environmental variables reflected by NMDS (final stress: 0.196) are shown in Fig. 2.2 and Table 2.6. The first axis, representing the principal floristic gradient, shows a high correlation with crop height, pH and height of the herb layer. NMDS axis 2 represents a gradient of conductivity (EC) and humus content. Crop height and mean annual temperature particularly show the strongest correlation, the latter with both axes. Other important variables that correlate significantly with both axes include the number of crops per year, crop cover, species richness and the type of season. Sites with less acidic soils (cluster C2) are found on the center-right part of the diagram. C2 plots are also characterized by short-statured plants with low cover, representing an early stage of the cultivation cycle, and by conspicuous species poverty (Table 2.5). The climate at C2 sites is hot tropical. Vegetation cluster C4 is located in the top left (Fig. 2.2) as its constituent species prefer moderately acidic soil conditions and comparatively lower temperatures. Vegetation is best developed in rather late stages of the crop cycle with increased canopy height and crop cover. The most characteristic features of cluster C1 are eutrophic soil conditions and relatively high species richness, placing it in the lower middle part of the diagram. C3, on the other hand, was only present in a small number of relevés and was characterized by very low species numbers, EC levels and humus contents. Cluster C4 was observed almost exclusively during the wet season whereas C2 and C3 were recorded mostly in the dry season. Many sites from Vietnam and the Philippines scored and intersected in the center of the diagram, possibly reflecting similar ecological conditions. Nonetheless, relevés from Vietnam are found more on the left side of the diagram whereas the Philippine sites, particularly those of Nueva Ecija, score on the right. Phytogeographic patterning seems to be more apparent on a regional scale as few clusters, but most subunits show clear preferences for particular study areas.

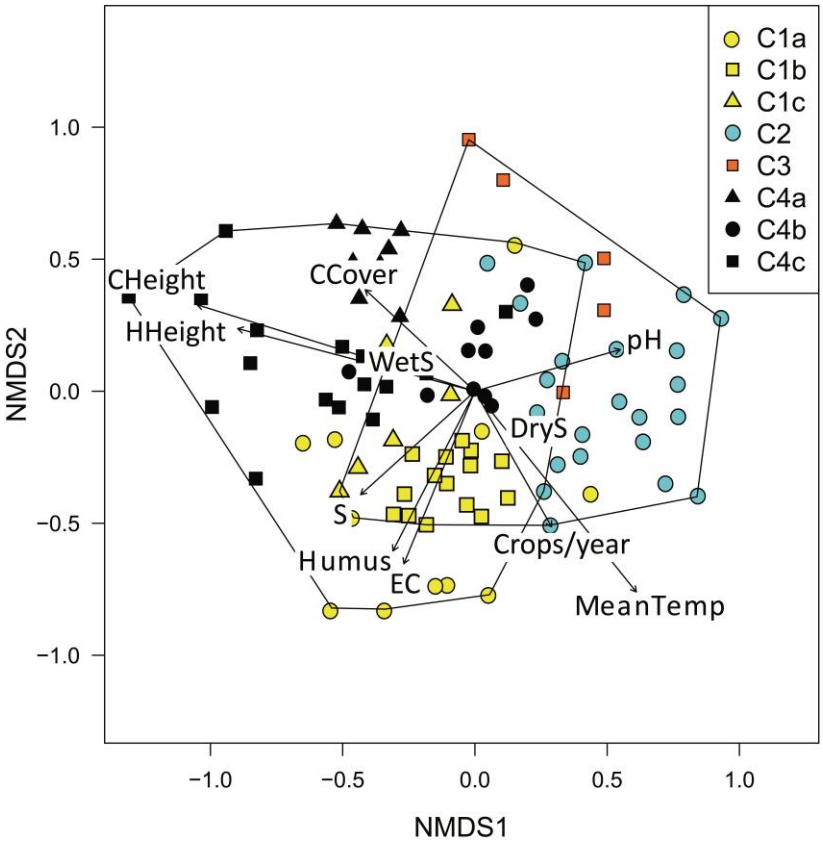

Fig. 2.2: NMDS ordination representing sites. Symbols indicate the different clusters (numbered as in the text and Tables 2.4 and 2.5), envelopes indicate the two countries (left = VN, right = PH). Environmental variables that correlate significantly ($p < 0.05$) with NMDS axes are indicated as arrows. (CCover = crop cover, CHeight = crop height, DryS = dry season, EC = electric conductivity, HHeight = height of herb layer, MeanTemp = mean annual temperature 2001–06, S = species richness (20 m²), WetS = wet season.)

2.4.4 Description of plant communities

C1: *Fimbristylis littoralis-Leptochloa chinensis* community (Appendix A.2, rel. 1−33)

This is the most widespread community type in the study area, though more commonly encountered in the Philippines. It was observed in very wet, muddy patches as well as on flooded ground, from the tropical Mekong Delta and Philippine lowlands up to the subtropical Red River Delta, and even in the cooler and more humid mountain provinces of both countries. The *Fimbristylis littoralis-Leptochloa chinensis* community prefers rather nutrient-rich sites, as indicated by the highest EC levels and humus contents measured during the field survey. Crop cover was on average rather low (60%), with sufficient light, space and nutrients available for weeds. It is the most species-rich community observed in the study area with vegetation plots consisting of up to 29 species (mean: 12, SD: 6.5). Many species of the *Cypero difformis-Echinochloetalia oryzoidis*, the order of Eurasian rice field vegetation, are common

differential taxa of this community: in order of frequency *Fimbristylis littoralis*, *Leptochloa chinensis*, *Alternanthera sessilis*, *Cyperus difformis*, *Lindernia antipoda*, *Ludwigia hyssopifolia*, *Eclipta prostrata*, *Ludwigia octovalvis*, *Ammannia baccifera*, *Sphenoclea zeylanica*, *Leersia hexandra*, *Ischaemum rugosum* and *Echinochloa colona*. It includes also a wide range of rarely found *Lythraceae* (*Ammannia microcarpa*, *A. multiflora*, *Rotala mexicana*, *R. indica*, *R. rosea* and *R. rotundifolia*).

Table 2.6: NMDS ordination was performed to visualize variation in plant community composition and the determinants. The table lists environmental variables (abbreviations used in Fig. 2.2 are given in brackets) that were fit a posteriori onto the ordination, their correlation with the NMDS axes, the goodness of fit (R^2) and the significance of each correlation (p; ** and *** mean significant at 1 and 0.1% levels, respectively). Centroids of each level of a categorical variable are listed separately before R^2 and p of the particular category is given.

	NMDS1	NMDS2	R^2	p	
Moisture	0.926	0.378	0.052	0.094	
pH	0.962	0.274	0.125	0.004	**
Electrical conductivity (EC)	-0.381	-0.925	0.192	0.001	***
C/N	0.446	0.895	0.006	0.761	
Humus	-0.452	-0.892	0.180	0.002	**
Mean annual temperature (MeanTemp)	0.629	-0.777	0.367	0.001	***
Crops/year	0.495	-0.869	0.134	0.003	**
Crop cover (CCover)	-0.731	0.682	0.123	0.004	**
Crop height (CHeight)	-0.956	0.293	0.469	0.001	***
Cover of herb layer	-0.954	0.299	0.043	0.121	
Height of herb layer (HHeight)	-0.968	0.251	0.332	0.001	***
Species richness (S)	-0.737	-0.676	0.134	0.004	**
Shannon diversity (H)	-0.992	-0.122	0.041	0.140	
Evenness (J)	0.235	0.972	0.042	0.127	
High landscape heterogeneity	-0.069	0.002			
Low landscape heterogeneity	-0.038	0.004			
Landscape heterogeneity			0.001	0.948	
Dry season (DryS)	0.241	-0.143			
Wet season (WetS)	-0.298	0.123			
Season			0.235	0.001	***

The C1 community can be further differentiated into the following subgroups:

C1a: *Fimbristylis littoralis-Leptochloa chinensis* subunit (rel. 1−11)

This is found in all regions except for VN3 and PH2, but primarily in lowland paddies. It probably represents the C1 community reduced to its basic species inventory at sites of higher agricultural intensity. Paddies were harvested usually two or three times per

year and their soils were mostly very strongly acidic. In addition, very high salt contents (max. EC: 2700 µS/cm) were recorded especially in the Mekong Delta.

C1b: *Ammannia baccifera-Leersia hexandra* subunit (rel. 12−27)

This subunit was mainly restricted to Laguna (PH1) lowlands and is differentiated by *Ammannia baccifera*, *Sphenoclea zeylanica*, *Leersia hexandra*, *Hydrolea zeylanica*, *Ischaemum rugosum* and *Echinochloa colona*. The local climate is hot tropical and the nutrient-rich soils are slightly acidic. Crop and herb layer were lower than in other sub units, and species numbers were relatively high (mean: 14, SD: 4).

C1c: *Azolla pinnata-Schoenoplectiella juncoides* subunit (rel. 27−33, photo in Appendix A.7c)

Mostly found in Ifugao (PH3), but also in the two other structurally diverse regions Vinh Phuc (VN2) and Lao Cai (VN3). Land use intensity is rather low, with the input of chemicals reduced and the particular paddies harvested only once per year. Characteristic species are *Echinochloa oryzoides*, *Azolla pinnata*, *Persicaria minor*, *Schoenoplectiella juncoides*, *Ageratum conyzoides*, *Cuphea carthagenensis*, *Cyperus pilosus* and *Cyperus haspan* (in order of frequency). C1c shows by far the highest species richness (mean: 20, SD: 6)

C2: *Paspalum distichum-Hydrolea zeylanica* community (Appendix A.3, rel. 69−97, photo in Appendix A.7d)

This community type is clearly concentrated in the province of Nueva Ecija (PH2), but was also observed locally in other lowland areas with hot and humid climate. The rice fields had flooded, slightly acid soils and showed rather low nutrient levels. The *Paspalum distichum-Hydrolea zeylanica* community emerges during an early stage of the crop cycle, indicated by low crop cover and low crop and weed height. The number of species was also low (mean: 4, SD: 2.9). The rhizomatous grass *Paspalum distichum* and the annual semi-aquatic herbs *Hydrolea zeylanica* and *Sphenoclea zeylanica* are common.

C3: *Echinochloa crus-galli* community (Appendix A.3, rel. 98−102)

This community type was found in a small number of paddy fields in Nueva Ecija (PH2) with a rather dense crop cover and highly inundated soils. At these sites of

intensive rice cultivation crops are harvested up to three times a year. Average EC level and humus content of inhabited paddies were rather low. It represents the most species-poor community of the vegetation survey (mean: 3, SD: 2.3). *Echinochloa crus-galli*, a cosmopolitan weed of various crops, was identified as its main diagnostic species. The fast-growing grass is capable of overtopping the rice plants and producing enormous quantities of seeds.

C4: *Rotala indica-Monochoria vaginalis* community (Appendix A.4, rel. 34−68)

This community type is restricted to Vietnam, with a preference for the subtropical north and the cooler, humid mountain sites. It grows on slightly wet to completely flooded ground with moderate acidity. Humus contents of the soils were rather low whereas a mean EC level of >200 µS/cm indicates a generally good availability of mineral nutrients. The *Rotala indica-Monochoria vaginalis* community was observed when rice plants were already in their ripening stage, with high average crop height (mean: 114 cm, SD: 16) and a moderately high crop cover. The community is characterized by relatively moderate species numbers (mean: 9, SD: 4) and a high percentage of short-lived helophytes such as *Rotala indica* and *Ludwigia prostrata*. The differential species *Alternanthera sessilis*, *Echinochloa oryzoides*, *Leptochloa chinensis*, *Lindernia antipoda*, *Ludwigia prostrata*, *Monochoria vaginalis*, *Rotala indica* and *Sagittaria trifolia* are diagnostic of the *Cypero difformis-Echinochloetalia oryzoidis*, Eurasian rice field vegetation. Other differential species of the C4 community are *Commelina diffusa* and the lemnids *Lemna aequinoctialis* + *minor*, *Spirodela polyrrhiza*, *Pistia stratiotes* and *Azolla pinnata*. In addition, many rare taxa belong here, e.g. several *Lythraceae* (*Ammannia multiflora*, *Rotala mexicana*, *R. ramosior*, *R. rosea* and *R. rotundifolia*).

The C4 community can be further differentiated into following subgroups:

C4a: *Sagittaria trifolia-Persicaria minor* subunit (rel. 34−42)

A typical subunit of the C4 community with the tuberous *Sagittaria trifolia* and the annual *Persicaria minor* occurs above 700 m. The mountain area of Lao Cai (VN3) is structurally diverse and has low land use intensity with only one rice harvest per year and low chemical input. Manual weeding was drastically increased on some fields. The mean annual temperature is cooler and soil acidity slightly lower than on sites of other

C4 subgroups. The lowest mean EC (76 µS/cm, SD: 46) indicates a lack of micronutrients in the local paddy soils, whereas crop cover was always high.

C4b: *Paspalum distichum-Hydrolea zeylanica* subunit (rel. 43−52)

The C4b subunit occurs preferentially in an agroenvironment of rather low land use intensity and medium landscape complexity such as in the subtropical lowlands of Vinh Phuc (VN2). Fields are planted with rice twice per year, but crop cover was rather low and height of the vegetation (crop and herbs) generally high. The differential species *Paspalum distichum*, *Hydrolea zeylanica*, *Lindernia anagallis* and *Ceratopteris thalictroides* distinguish C4b from other subgroups of this cluster.

C4c: *Spirodela polyrrhiza-Pistia stratiotes* subunit (rel. 53−67)

The differential species *Lemna aequinoctialis*, *Spirodela polyrrhiza*, *Pistia stratiotes* and *Azolla pinnata* prefer a warm subtropical climate and were found mainly in the lowlands of the Red River valley in Hai Duong (VN1). Co-occurrences of these lemnids are not restricted to rice agroecosystems as similar species combinations are known from other tropical freshwater habitats around the world (Landolt 1999). Their vegetative reproduction allows rapid colonization of new waters. Farmers value them as a source of forage. They were typically complemented by the two helophytes *Alternanthera philoxeroides* and *Lindernia procumbens*. Acidity of the soils varied a lot, EC levels were increased.

2.5 Discussion

2.5.1 Diversity and composition of local rice weed species and life forms

Our records of Vietnamese and Philippine rice fields showed rather low species richness and cover. This corresponds with the finding of Miyawaki (1988) that rice weed communities are often fragmentary and characterized by comparatively low species numbers. Nevertheless, the total number of species encountered during our survey was about as high as those found in similar studies from Southeast and Central Asia (Nowak et al. 2013, 2015, 2016; Kumalasari 2014) whereas rice phytocoenoses in the temperate to meridional climate zones from southern Europe, California and Japan showed lower species richness (Bolòs & Masclans 1955; Miyawaki 1960; Barrett & Seaman 1980; Carretero 1989). In mountain areas relatively high total species numbers were found (68

species in 19 relevés), whereas the mean number of species did not differ significantly from lowland paddies. Relevés of the rice terrace landscapes reveal higher species turnover (and gamma diversity), probably as a result of increased landscape heterogeneity, but studies are currently in progress to clarify causality (Fried et al., in press, chapter 4). The species richness estimation (Fig. 2.1a) suggests that the species pool of upland rice fields is larger than that of the lowlands. The number of relevés was lowest in region VN4 due to the inability to locate rice fields with weedy vegetation in these highly intensive production sites.

Most farmers and the general public perceive rice weeds as a serious impediment to rice production and much research has been carried out to improve methods of weed control (e.g. De Datta 1981; IRRI 1983; Moody 1989). On the other hand, land use intensification and conversion of land to monoculture are among the main drivers of global biodiversity loss. Concerns about the loss of agrobiodiversity have increased as plants and animals of agricultural landscapes can provide beneficial services related to pest control, nutrient cycling, water regulation, pollination etc. (Gonthier et al. 2014). Additionally, in mid- and upland areas agrobiodiversity is threatened by abandonment of agricultural land and agrarian depopulation (Nowak et al. 2013; Koyanagi et al. 2014).

Rice landscapes host a variety of specialized species, many of which are globally rare (IUCN 2015; Nowak et al. 2015). The species composition in Vietnamese and Philippine rice fields is characterized by a high percentage of graminoids and regular occurrences of *Lythraceae*, *Asteraceae*, *Linderniaceae*, *Araceae* and *Onagraceae* species. These include many notorious rice weeds, but also taxa that are uncommon or rare in the study area, e.g. *Ammannia coccinea*, *A. microcarpa*, *A. multiflora*, *Lindernia rotundifolia*, *L. procumbens*, *Rotala mexicana*, *R. ramosior*, *R. rosea* and *R. rotundifolia*. Most of these appear to be declining globally (IUCN 2015) and this may become an issue for nature conservation. In total, 60 red-listed species were recorded, highlighting the need for intensified research on the local and regional species diversity and distribution. *Cyperus digitatus*, *C. distans*, *Ludwigia adscendens*, *Rotala mexicana*, *R. rosea*, *R. rotundifolia* and *Schoenoplectiella mucronata* are now known to be threatened in Japan (Biodiversity Center of Japan, Ministry of Environment 2013). Efforts must be undertaken if the conservation status of these species is to be improved and their populations and habitat conditions preserved. Importantly, until now, little is

known about the ecosystem functions that the above-mentioned taxa provide for the local rice landscapes. The situation is aggravated if we consider that the global expansion of agriculture has led to shifts in the distribution and range of many plant and animal species (Martin & Sauerborn 2013), and that wetlands seem to be especially vulnerable to invasions of alien plants (Zedler & Kercher 2004). Rice fields constitute both source and sink habitats for invasive plants. Consequently, studies concerning invasion risks of the Southeast Asian rice weed flora and subsequent interactions in community composition are urgently needed.

Our findings on the life form composition correspond to previous observations in Japan and southern Europe (Bolòs & Masclans 1955; Miyawaki 1960). Annual amphibious and free-floating plants are the predominant life forms. They are best adapted to the aquatic to semi-aquatic conditions of the paddies, the short rice cultivation cycle and related weeding practices. Many hydro- and helophytes indicate the close floristic relationship of rice weed communities with the aquatic and amphibious vegetation of natural wetlands. This is further supported by the high percentage of species capable of adjusting their life cycle in response to their environment.

2.5.2 Community composition and environmental conditions

The rice weed communities of the *Oryzetea sativae* in Vietnam and the Philippines are floristically related to syntaxa of semi-natural wetlands and of agrarian landscapes, e.g. to the *Lemnetea*, *Bidentetea*, *Phragmito-Magno-Caricetea*, *Potametea*, *Charetea* or *Stellarietea*. Such links have been shown in several studies of rice fields around the world (e.g. Bolòs & Masclans 1955; Miyawaki 1960; Piccoli & Gerdol 1981; Kim 2001). Due to their floristic similarity with other tropical rice weed communities in Thailand, Indonesia and Nepal (Kumalasari 2014; Nowak et al. 2015, 2016) the Vietnamese and Philippine communities may be classified in the alliance *Ludwigion hyssopifolio-octovalvidis* Nowak et al. 2015. Particularly the *Fimbristylis littoralis-Leptochloa chinensis* community shows a close relation to the *Fimbristylido miliaceae-Sphenocleetum zeylanicae* Nowak et al. 2015 as well as to the *Ischaemo rugosi-Cyperetum pulcherrimi* Nowak et al. 2015, both known to occur in Thailand (Nowak et al. 2015). The fact that *Hydrolea zeylanica* has not been mentioned to date in any known syntaxon of rice weed communities, underlines the lack of knowledge on the subject, as it is common in rice paddies, at pond margins, streamsides and other wet

habitats from Australia to Nepal (eFloras 2008). *Echinochloa crus-galli* is a global, noxious weed in various agroecosystems (Holm 1977) and occurs frequently also in other syntaxa, e.g. the *Bidentetea tripartitae*, *Sisymbrietea officinalis* or *Stellarietea mediae* (Klotz et al. 2002). Thus, it may be assumed that the *Echinochloa crus-galli* community is a truncated, species-poor fragment of the *Cypero difformis-Echinochloetalia oryzoidis* at especially intensively managed rice cultivation sites. It may also represent a form of the *Paspalum distichum-Hydrolea zeylanica* community, occurring during a later stage of the crop cycle with high crop cover and height.

Floristic composition and distribution of weeds often serve as indicators of field conditions as even minor changes in the ecoclimatic, edaphic, and agrobiotic factors or tillage treatments cause important changes in plant associations (Moody & Drost 1983). Among the climatic factors we identified the mean annual temperature as an important discriminating factor for the differentiation of rice weed communities. Species composition changes with increasing elevation and distance from the equator, where genera in rice fields are common in temperate regions, e.g. *Cardamine*, *Hypericum*, *Plantago* or *Potentilla*. Temperature triggers germination, emergence and growth rate of rice weeds differently (Smith, Jr. 1983). An influence of elevation on the differentiation of rice weed communities is also documented from Indonesia (Kumalasari 2014), Tajikistan (Nowak et al. 2013) and Nepal (Nowak et al. 2016).

De Datta and Feuer (1975) stated that "inherent fertility levels and chemical composition of soils often explain yield differences and even cultural practices". We found a strong relation between weed composition and soil acidity, EC and humus contents. However, in Java (Kumalasari 2014) and in Tajikistan (Nowak et al. 2013) neither pH nor nutrients show strong effects whereas in Nepal soil fertility plays a major role (Nowak et al. 2016). Further vegetation analyses should include soil measurements to disentangle interactions between soil, management, crop and weeds.

Distinct levels of species richness are documented from Nepalese and Thai rice phytocoenoses (Nowak et al. 2015, 2016). In our survey, variation in rice weed species richness at the community level reflects cultivation intensity and status of the rice fields. Additionally, observed gradients of crop cover, crop height and herb height show that the species composition varies in accordance with the phenology of the rice plant. An adequate survey of rice phytocoenoses should therefore comprise repeated sampling

during the cropping season, ideally in all cultivation cycles, to reveal seasonal changes in the rice weed flora (Moody & Drost 1983). Such turnover in weed community composition may be attributable to temperature seasonality (as in our subtropical areas VN1 and VN2) and/or to agricultural management and crop rotation. Rainfall and humidity should be less important in irrigated landscapes of permanent water availability. Nonetheless, grasses, sedges and broadleaved weeds react differently under soil moisture regimes (De Datta 1981; Juraimi et al. 2011) and seasonal variation in community composition of tropical rice ecosystems occurs if water availability is limited (cf. Kumalasari 2014). Although soil moisture regime is widely accepted as a major factor influencing the weed flora (e.g. De Datta 1981; IRRI 1983; Tomita et al. 2003; Juraimi et al. 2011; Kamoshita et al. 2014; Kumalasari 2014; Nowak et al. 2015, 2016), no correlation between water regime and community composition was found in our study, which is probably due to the minor differences of observed water levels. Despite the farmer interviews, the information gathered on flooding times was too vague for proper evaluation. We believe that extensive studies like in Thailand (Tomita et al. 2003) are required to assess the influence of the water table on the vegetation of paddies more adequately. The grain-size of the soils seems to be a less decisive parameter for the occurrence of a particular community, as all vegetation clusters comprised a wide range of textural classes from sandy loam to heavy clay.

2.5.3 Weed control and cultivation methods

Paddy weeds are mostly controlled by puddling/harrowing, herbicide application and hand weeding (Table 2.2). Very seldom are they cut and rarely do animals graze the paddies in the study area (after harvest or before planting). This is in contrast to land use habits such as in Java, Indonesia (Kumalasari et al. 2014). Differences in weed control were found to be most pronounced between mountainous and lowland regions. Farmers in the highlands of both countries are managing their rice fields in a more traditional manner and mostly do not apply herbicides. Various works describe similar characteristics of mountainous (rice) agroecosystems such as the use of traditional upland rice cultivars, reduction of synthetic fertilizers and herbicides, and manual weed control (De Datta 1981; Roder 1997; Roder et al. 1997; Galinato et al. 1999; Husson et al. 2001; Doanh & Tuan 2004; Paudel 2011; GRiSP 2013). The paddies in Lao Cai (VN3) are especially subject to intensive monitoring and frequent hand weeding (Table 2.2). Another characteristic of the mountain areas is the restriction to one rice crop per

year, whereas in all other study regions usually two harvests per year are possible due to climate. The most intensive rice production was observed in the Mekong delta, with three crop cycles per year, frequent application of herbicides and other methods of weed control, leading to severely decreased plant diversity. The influence of the method of crop establishment could not be analyzed with multivariate approaches as rice plants in the study areas were almost always transplanted.

2.6 Conclusions

Vietnam and the Philippines are amongst the countries most severely affected by biodiversity loss. For Vietnam, rapid growth of agricultural production (69% from 1995–2005) has been identified as a major threat to biodiversity conservation (Sodhi et al. 2010). Efforts to improve the sustainability of rice agriculture are increasing recently (Yamada et al. 2007; Rossi et al. 2015; Westphal et al. 2015). Weed community composition is probably the best and most reliable indicator of management intensity. At the same time, it provides information about environmental and biogeographical conditions. In order to adequately assess the functioning of entire rice agroecosystems and landscapes it is advisable to include biophysical, gradient-based studies of adjacent plant assemblages and structures. Research on the bunds as a distinct habitat and as an important element of landscapes used for rice cultivation, has been completed in a separate study (Fried et al. 2018). Additional studies of ditches and the rice terrace walls in representative mountainous regions are planned to complement our knowledge of the Southeast Asian rice landscapes.

Author contributions

E.B. and I.K. planned the research, O.F. and J.S. conducted the field sampling, O.F. performed the statistical, taxonomical and edaphic analyses and led the writing, while all authors critically revised the manuscript.

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Chapter 3:

Plant diversity and composition of rice field bunds in Southeast Asia

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Abstract

Which plant species can be found on rice field bunds and what are the prevailing life forms? Which plant communities occur and what are the main environmental drivers and phytogeographic patterns shaping these communities? How do species diversity and composition differ between bunds and paddies? To answer these questions, 133 vegetation relevés using the Braun-Blanquet method were collected in lowlands and uplands of Vietnam and the Philippines between 2012 and 2015. Soil samples were collected and farmers were interviewed. Properties of soil, climate, and geography were assessed, further structural parameters, landscape heterogeneity, seasonality, management and intensity of cultivation. Hierarchical UPGMA cluster analysis and NMDS ordinations were performed to visualize variation in plant community composition and the determinants. We found 302 vascular plant species, of which 94 species are red listed by the IUCN (under category "Least concern"). Therophytes and helophytes are the prevailing life forms. Six clusters of plant communities were classified and temperature, soil acidity, land use intensity and nutrient availability were identified (according to relevance) as explanatory variables. Bunds revealed higher species richness than paddies and bunds in mountain areas were more species-rich than those in the lowlands. We conclude that the composition of bund communities provides valuable information on environmental and biogeographical conditions of the local rice landscapes, and that it is probably the best applicable and most reliable indicator of management intensity.

3.1 Introduction

Rice is the staple food for most people on Earth and the most important source of employment and income for rural people, particularly in (sub)tropical Asia (GRiSP 2013). Global rice production increased to 496.7 million tonnes (milled basis) until the end of 2016, to which Asia contributed about 90% (449.1 million tonnes) (FAO 2016). Especially Southeast Asia's growing populations rely substantially on their rice yields to meet an increasing demand for food and economical security. In 2013, per capita rice consumption in Vietnam and the Philippines totaled 144.6 kg and 119.4 kg per year, respectively. Southeast Asia's areas of rice cultivation added up to 48.3 million ha in 2014, comprising 7.8 million ha in Vietnam and 4.7 million ha in the Philippines (FAO 2020). Apart from its nutritional and agronomic importance, rice cultivation is also deeply ingrained in the life and cultural habits of the local people (e.g. Fernando 1995; Pretty 2002; GRiSP 2013).

Rice is grown in a wide range of environments that are mostly classified by hydrological characteristics (GRiSP 2013). Bambaradeniya & Amerasinghe (2003) defined rice fields as temporary, seasonal wetland ecosystems agronomically managed with varying intensities. Several studies describe these ecosystems in detail, their biotic and abiotic factors, agricultural management, nutrient cycles, and biodiversity (e.g. Heckman 1979; De Datta 1981; Moody 1989; Fernando 1995; FAO 2000; Bambaradeniya & Amerasinghe 2003; GRiSP 2013; Fried et al. 2017), but the knowledge of plant communities in rice ecosystems, their diversity, composition, dynamics and distribution is still insufficient (Barrett & Seaman 1980; Moody & Drost 1983; Nowak et al. 2016). Mainly three different habitat types may be distinguished in rice agroecosystems and each supports distinct weed communities: the field proper (paddy), the bund (ridge, dyke, levee) and the ditch (water supply canal) (Barrett & Seaman 1980; Bambaradeniya & Amerasinghe 2003).

Detailed phytosociological research has yet been focused on the plant composition of paddies (Bolòs & Masclans 1955; Tallon 1958; Miyawaki 1960; Piccoli & Gerdol 1981; Carretero 1988, 1989; Parras & Lorca 1993; Kolbek et al. 1996; Kim & Nam 1998; Kim 2001; Turki & Sheded 2002; García & Benzal 2009; Nowak et al. 2013, 2015, 2016; Kumalasari 2014; Fried et al. 2017). Less studies dealt with the floristic diversity and composition on bunds or merely touched upon these topics (e.g. Bambaradeniya et al.

1998; Fukamachi et al. 2005; Iiyama et al. 2005; Kawano et al. 2009; Matsumura & Takeda 2010; Kosaka et al. 2013; Yasuda et al. 2013; Koyanagi et al. 2014; Kumalasari 2014; Nemoto & Otsuka 2014). Many of these have shown that the vegetation is more abundant and diverse than in paddies, but detailed descriptions of bund communities and their composition have never been in focus.

Awareness is growing that rice agroecosystems offer a variety of services (GRiSP 2013). The bunds have a major part in this as they provide several important functions in cultural landscapes (e.g. Fukamachi et al. 2005). Apart from being used as footpaths and water barriers, they also possess sociocultural value as borders of a farmer's property. Amount, extent, location and state of a farmer's rice field(s) can provide information on wealth and social rank. Farmers and owners might fear a loss of reputation if the vegetation on their field margins grows too "wild". But bunds and their vegetation are also appreciated for aesthetic and cultural values (Westphal et al. 2015), particularly in traditionally managed rice terrace landscapes (Iiyama et al. 2005). Many rice weeds are a source of medicine, forage, food or other purposes (Raju et al. 2001; eFloras 2008; IUCN 2015), and selling collected herbs can increase the income of rural people (Kosaka et al. 2013). Differences in behavior and valuation influence in turn the handling, control and, consequently, occurrence of species. A proper vegetation management on bunds can attract crop pollinators and other beneficial arthropods (e.g. pest antagonists) while simultaneously reducing pesticide inputs and labor costs (e.g. Way & Heong 1994; Ichihara et al. 2015; Westphal et al. 2015). Additionally, bunds offer refuge to endangered organisms (Naito et al. 2013). We assume that bunds are important source, sink, and corridor habitats for specialized rice weeds and plant communities.

In this paper, we focus on the abundance, distribution and composition of vascular plant communities on bunds adjacent to paddies in Vietnam and the Philippines to complement our knowledge on the phytocoenoses of Southeast Asian rice landscapes (Fried et al. 2017). We pose the following research questions: (1) Which plant species can be found on the rice field bunds in selected lowland and upland areas of Vietnam and the Philippines? (2) Which plant communities occur and what are the prevailing life forms? (3) What are the main environmental drivers and phytogeographic patterns shaping these communities? (4) In the agroecosystem context, how does the bund

vegetation in terms of species diversity and composition compare to that of adjacent paddies?

3.2 Study area

Seven study regions were surveyed in Vietnam and the Philippines, each covering 15 km x 15 km (Fig. 1.7, Table 1.1). The local climate, geography, landscape heterogeneity, and land use intensity has been treated extensively in chapter 1.5.1.

The bunds in the study area are typically 25–50 cm wide at the top and 10–25 cm high. In the flat lowlands, they embank paddies and are usually constructed with soil, whereas on mountain slopes they are strengthened with stones and line terraced fields. They border other paddies, crop fields, grasslands, gardens, agroforests, forests, ditches and water bodies, pathways or concrete structures (roads and buildings). Bunds and their vegetation are subject to regular and irregular disturbances through weed control (with varying intensities) and repairing measures in the whole region, while damage through heavy flooding during erratic tropical storms occurs sporadically. Arable or horticultural crop plants are infrequently cultivated on bunds in the Mekong and mountain areas.

3.3 Methods

3.3.1 Data collection

A total of 133 vegetation relevés was collected on rice field bunds during a four-year period (2012–2015). Each of the seven study areas was represented by 10 to 35 relevés (Table 3.1). The survey was designed to detect possible effects of landscape heterogeneity on the vegetation (Klotzbücher et al. 2015; Settele et al. 2015). Bunds were sampled preferentially according to the accessibility of rice fields and approachability of farmers during the periods of sampling. Field margins between paddies and other structures (e.g. gardens or ditches) were included in the sampling. Vascular plant species were recorded together with their cover/abundance values using the nine-class Braun- Blanquet scale (Reichelt & Wilmanns 1973). Bryophytes were not included in the survey. Relevés were located on top of bunds, but to capture the variation of each bund in terms of shape and stability, five randomly stratified 2 m^2 subplots were laid out around each rice field. Cover-abundances were transformed into

Table 3.1: The vegetation on Southeast Asian rice field bunds was studied between 2012 and 2015. Study regions and important corresponding attributes related to geography, climate and management are listed. Additionally, the number of collected relevés, the number of recorded taxa and the percentage of recorded taxa from the total species pool assessed during the study are given for each region. Information on land use intensity and structural diversity is taken from Settele et al. (2013).

Country code	Study area ID	Province	High-/ Lowland	Latitude range (WGS84,°)	Longitude range (WGS84,°)	Land use intensity	Structural diversity	Elevation range of study sites (m)	Mean annual temperature range (°C)	Num-ber of relevés	Num-ber of taxa	Taxa (%)
PH	PH1	Laguna	low	14.11–14.23	121.30–121.41	medium - high	medium	8–290	26.4–27.6	20	122	41
	PH2	Nueva Ecija	low	15.51–15.75	120.84–121.01	medium - high	low - medium	24–80	26.7–27.1	35	99	33
	PH3	Ifugao	high	16.86–16.93	121.05–121.14	low	high	780–1182	17.6–22.1	18	121	40
VN	VN1	Hai Duong	low	20.94–21.09	106.35–106.44	medium - high	low - medium	0–11	23.9–24.2	20	105	35
	VN2	Vinh Phuc	low	21.30–21.37	105.70–105.74	low - medium	medium	4–34	24.4–24.9	20	113	38
	VN3	Lao Cai	high	22.30–22.41	103.84–103.91	low	high	725–1390	17.6–22.0	10	98	33
	VN4	Tien Giang	low	10.37–10.44	106.06–106.13	high	low - medium	3–9	28.0–28.1	10	38	13
Total	-	-	high + low	10.37–22.41	103.84–121.41	low - high	low - high	0 - 1390	17.6 - 28.1	133	302	100

percentages (r = 0.1, + = 0.5, 1 = 2.5, 2m = 2.5, 2a = 10, 2b = 20.5, 3 = 37.5, 4 = 62.5, 5 = 87.5) (Dierschke 1994). The species inventory of the five subplots was pooled and percentages were averaged to represent relevés of 10 m^2 size per bund. Altitude and geographical coordinates of the plots were determined with a GPS (Garmin eTrex Vista® HCx) device.

The following works were used for plant identification: Harada et al. 1987, 1993; Soerjani et al. 1987; Pancho & Obien 1995; Cook 1996; Ho 1999, 2000, 2003; Nguyen 2002; Le 2007; Nguyen & Nguyen 2007; eFloras 2008. Voucher specimens of each plant species were collected and stored in the herbarium GOET (University of Göttingen). Separate cover-abundance estimation for *Lemna aequinoctialis* and *L. minor* was not feasible, hence the species were treated collectively. Nomenclature follows The Plant List (2013) for taxa and Mucina et al. (2016) for syntaxa.

Plant life form classes follow Ellenberg & Mueller- Dombois (1967), except for helophytes which represent partly submerged, amphibious plants irrespective of life span (Appendix A.1). Some species were assigned to more than one life form, e.g. annual helophytes or species that occur as annual and perennial plants depending on local conditions. Each life form of such species was counted separately in the calculation of life form percentages.

Mixed soil samples were collected from five spots of each bund (10–20 cm depth at each subplot) and later analyzed in laboratories of Göttingen University. Electrical conductivity (EC) was measured with a conductivity gauge of the type pH538 (WTW GmbH) in the supernatant suspension of a 1:2.5 soil:H_2O mixture, before assessing the soil pH with a pH meter of the type pH358 (Krannich GmbH & Co.KG). Contents of organic carbon (C_{org}) and total nitrogen (N_{total}) were measured with the Dumas combustion method using a VARIO MAX (elementar), humus content was estimated afterwards (C_{org}*1,725). Texture was checked on a moist sample of fine earth and through visible characteristics (FAO 2006).

Three categories of soil moisture with increasing water content were distinguished: 1 - moist but solid soil; 2 - wet and soft soil; 3 - very wet and muddy soil with interspersed puddles.

Farmers of the surveyed rice fields were interviewed using standardized questionnaires on timing and practice of weed control on the bunds and the number of crop cycles per year.

Monthly mean temperatures from the years 2001–2006 were supplied by the Potsdam Institute for Climate Impact Research and are based on a time-series data set (CRU TS 3.0) provided by CRU et al. (2008).

3.3.2 Data analyses

The cultivated species as well as singletons and doubletons were eliminated from the data set before excluding plots without weeds. The species data of the remaining 128 relevés were Hellinger transformed (c.f. Legendre & Gallagher 2001) and hierarchical UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis based on Euclidean distances applied. Synoptic tables (Tables 3.2 and 3.3) were prepared using JUICE 7.0 (Tichý 2002). Differential taxa were identified with the algorithm of Tsiripidis et al. (2009). Main diagnostic species are exclusively positively differentiating for the particular cluster and highlighted in the ordered relevé tables (Appendix A.8–10).

Nonmetric multidimensional scaling (NMDS), commonly regarded as the most robust unconstrained ordination method in community ecology (Minchin 1987), was performed to visualize differences in plant community composition along gradients of environmental and other variables, i.e. elevation, temperature, soil properties (moisture, pH, EC, C_{org}/N_{total}, humus content), geographic location, landscape heterogeneity (high vs. low), season (dry vs. wet), number of crops/year, cover of herb layer, and species diversity. A Wisconsin double standardization and a square root transformation of the original cover-abundances were performed before NMDS as they improved the ordination results. NMDS ordinations (based on Bray-Curtis dissimilarities and random starting configurations) were optimized for three dimensions after examination of a scree stress plot and by visual inspection and comparison of resulting ordination graphs. The strength of the ordination was assessed using the final stress. The first two axes of an NMDS do not necessarily reflect the longest floristic gradients as is the case with most other indirect ordination methods. Therefore, two ordination graphs were chosen for optimal visualization of the ordination results (Fig. 3.2). Environmental variables were fit *a posteriori* onto the ordination (Fig. 3.2b), using 999 permutations.

"Elevation" was excluded due to strong negative correlation with "mean annual temperature" (r = 0.86, p < 0.001). Insignificant variables (p > 0.05) were also excluded. Information on weed control is summarized in Appendix A.11.

All multivariate analyses of the data were performed with the packages *vegan* (Oksanen et al. 2019) and *cluster* (Maechler et al. 2015) of the R software (R Core Team 2018). Figures were post-processed using Inkscape (Inkscape Team 2015).

3.4 Results

3.4.1 Floristic diversity

Three hundred and two plant taxa (incl. nine cultivated plants) were recorded on the rice field bunds of the study areas, belonging to 177 genera and 59 families (Tab. 3.1, Appendix A.5). Most taxa belong to the families *Poaceae* (58), *Asteraceae* (31), *Cyperaceae* (24), *Fabaceae* (19) and *Linderniaceae* (11). The most common species were *Eclipta prostrata* (106 relevés), *Fimbristylis littoralis* (106), *Alternanthera sessilis* (97), *Commelina diffusa* (87), *Ludwigia hyssopifolia* (85), *Kyllinga brevifolia* (83), *Cynodon dactylon* (82), *Eleusine indica* (81), *Lindernia antipoda* (77) and *Paspalum conjugatum* (72). Character species of the phytosociological class *Oryzetea sativae* were typically well represented (e.g. *Alternanthera sessilis*, *Fimbristylis littoralis*, *Kyllinga brevifolia*, *Lindernia antipoda* and *Ludwigia hyssopifolia*). They were mostly accompanied by species of the *Eragrostietalia*, ruderal vegetation rich in C4 grasses, with several of them being especially competitive in trampled habitats (e.g. *Cynodon dactylon*, *Digitaria ciliaris*, *Eleusine indica*, *Paspalum conjugatum*). Mostly annual species of genera common in the *Polygono-Poetea annuae* (*Plantago*, *Polygonum*) and *Bidentetea tripartiti* (*Bidens*, *Eclipta* and *Persicaria*), and perennial, mostly graminoid, species of the *Phragmito-Magno-Caricetea* (*Eleocharis*, *Leersia*, *Oenanthe* etc.) were interspersed; further the free floating pleustons of the *Lemnetea* (*Azolla*, *Lemna*, *Spirodela*, *Pistia* and *Eichhornia*) in temporary puddles.

Several characteristic highland species were recorded, e.g. *Fimbristylis dichotoma*, *Cuphea carthagenensis*, *Cyclosorus interruptus*, *Equisetum ramosissimum* ssp. *debile*, *Hypericum japonicum*, *Hydrocotyle pseudoconferta*, *Potentilla kleiniana*, *Plantago asiatica* and *Rorippa indica*, whereas other species were mostly encountered on lowland bunds, e.g. *Cynodon dactylon*, *Hydrocotyle sibthorpioides*, *Leptochloa chinensis*,

Marsilea minuta, *Panicum repens* and *Rotala rotundifolia* (Table 3.2). Most diagnostic species occur in both countries, with some of them encountered in this study on the bunds of only one country, e.g. *Hydrocotyle pseudoconferta*, *Ludwigia prostrata* and *Potentilla kleiniana* only in Vietnam, *Cuphea carthagenensis*, *Equisetum ramosissimum* ssp. *debile* and *Hyptis brevipes* in the Philippines.

Table 3.2: Synoptic table showing common and diagnostic species on Southeast Asian rice field bunds with their constancies (%) in each country and altitudinal level. Differential taxa (dark-grey bold = positively differentiating, light-grey italic = negatively differentiating, grey bold italic= positive-negatively differentiating) were identified with the algorithm of Tsiripidis et al. (2009).

Country	**PH**		**VN**	
High-/Lowland	**low**	**high**	**low**	**high**
Number of relevés	55	18	45	10
Taxon				
Hyptis brevipes	**35**	**28**	*0*	*0*
Ludwigia octovalvis	**44**	**78**	*7*	*0*
Ludwigia prostrata	*0*	*0*	**76**	**60**
Paspalum distichum	*22*	44	**93**	**70**
Persicaria hydropiper	*0*	*0*	**22**	**20**
Persicaria minor	*0*	*17*	**40**	**80**
Cynodon dactylon	**82**	*11*	**78**	*0*
Leptochloa chinensis	**47**	*6*	**80**	*10*
Panicum repens	**36**	*6*	**82**	*10*
Cyperus iria	**47**	*11*	**47**	40
Oldenlandia corymbosa	**40**	*0*	**47**	*0*
Ipomoea aquatica	**35**	*0*	**24**	*0*
Eriochloa procera	**25**	*0*	**20**	*0*
Hypericum japonicum	*0*	**67**	*7*	**100**
Fimbristylis dichotoma	*5*	**56**	*11*	**70**
Rorippa indica	*13*	**72**	*7*	**40**
Centella asiatica	*18*	**67**	42	**60**
Arthraxon spec.	*0*	**56**	*0*	**20**
Crassocephalum crepidioides	*2*	**22**	*0*	**40**
Oenanthe javanica	*0*	**33**	*2*	**30**
Lindernia setulosa	*0*	**33**	*0*	**20**
Ischaemum rugosum	**47**	*0*	*9*	*0*
Cyanthillium cinereum	**44**	*6*	18	*0*
Cyperus rotundus	**40**	*6*	11	*0*
Hydrolea zeylanica	**27**	*0*	11	*0*
Polytrias indica	**25**	*0*	*0*	*0*
Brachiaria mutica	**24**	*0*	*2*	*0*
Sphenoclea zeylanica	**22**	*0*	2	*0*
Cleome rutidosperma	**20**	*0*	7	*0*
Heliotropium indicum	**20**	*0*	4	*0*
Melochia corchorifolia	**20**	*0*	2	*0*
Cuphea carthagenensis	*0*	**100**	*0*	*0*

Table 3.2: (continued)

Country	**PH**		**VN**	
High-/Lowland	**low**	**high**	**low**	**high**
Number of relevés	55	18	45	10
Cyclosorus interruptus	*0*	**67**	*9*	*0*
Equisetum ramosissimum ssp. *debile*	*0*	**67**	*0*	*0*
Gonostegia hirta	*7*	**67**	*0*	*20*
Imperata cylindrica	16	**67**	*4*	30
Paspalum scrobiculatum	*9*	**56**	*13*	*10*
Colocasia esculenta	*5*	**56**	29	*10*
Pycreus flavidus	*0*	**50**	*0*	*0*
Euphorbia hirta	16	**50**	*4*	*0*
Digitaria violascens	*0*	**39**	7	20
Cardamine hirsuta	*0*	**39**	*0*	10
Pseudelephantopus spicatus	16	**39**	*0*	*0*
Mikania cordata	11	**33**	*0*	*0*
Hyptis capitata	5	**28**	*0*	*0*
Apluda mutica	*0*	**22**	*0*	*0*
Galinsoga parviflora	*0*	**22**	*0*	10
Hydrocotyle sibthorpioides	*2*	*0*	**69**	*0*
Rotala rotundifolia	*0*	*0*	**58**	*0*
Axonopus compressus	*18*	*0*	**56**	*0*
Marsilea minuta	*0*	*0*	**56**	*0*
Centipeda minima	*0*	*0*	**49**	*10*
Lindernia procumbens	*2*	*11*	**42**	*0*
Panicum auritum	*0*	*0*	**40**	*0*
Echinochloa crus-galli	16	*0*	**33**	*0*
Ceratopteris thalictroides	*2*	*0*	**31**	*0*
Lemna aequinoctialis + minor	*0*	*0*	**29**	10
Gonostegia pentandra	*2*	*0*	**27**	*0*
Lindernia crustacea	11	11	**27**	*0*
Scoparia dulcis	16	*0*	**22**	*0*
Phyllanthus debilis	18	*0*	**20**	*0*
Pistia stratiotes	4	*0*	**20**	*0*
Alternanthera philoxeroides	4	*0*	**20**	*0*
Rotala indica	*0*	*6*	*20*	**100**
Cyperus haspan	*0*	*11*	*29*	**90**
Hydrocotyle pseudoconferta	*0*	*0*	*0*	**80**
Murdannia nudiflora	*5*	*0*	*11*	**80**
Potentilla kleiniana	*0*	*0*	*0*	**80**
Pseudognaphalium hypoleucum	*0*	*6*	*0*	**70**
Oxalis corniculata	*2*	33	16	**70**
Cyperus difformis	35	*17*	33	**70**
Lamiaceae spec. (1)	*0*	*0*	*0*	**70**
Plantago asiatica	*0*	*0*	*0*	**70**
Juncus prismatocarpus	*0*	*0*	*7*	**60**
Pycreus sanguinolentus	*0*	*0*	*7*	**60**

Table 3.2: (continued)

Country	**PH**		**VN**	
High-/Lowland	**low**	**high**	**low**	**high**
Number of relevés	55	18	45	10
Setaria pumila	*0*	*0*	*0*	**60**
Selaginella ciliaris	*0*	*0*	*0*	**50**
Desmodium spec.	*0*	*0*	*0*	**40**
Lobelia nummularia	*0*	*0*	*0*	**40**
Mazus pumilus	*5*	17	29	**40**
Paspalum urvillei	*0*	*0*	*0*	**40**
Schoenoplectiella juncoides	*0*	*6*	*0*	**40**
Persicaria nepalensis	*0*	*0*	*0*	**30**
Ranunculus cantoniensis	*0*	*0*	*0*	**30**
Sagittaria trifolia	*0*	*0*	11	**30**
Alternanthera sessilis	**84**	**50**	**91**	*10*
Paspalum conjugatum	**75**	**83**	**36**	*0*
Ludwigia hyssopifolia	**69**	**39**	**89**	*0*
Eleusine indica	**60**	**94**	**64**	*20*
Sacciolepis indica	*0*	**39**	**29**	**30**
Cyperus pilosus	*2*	**50**	**24**	**30**
Digitaria ciliaris	*20*	**67**	**60**	**100**
Drymaria cordata	*7*	**50**	**36**	**60**
Lindernia anagallis	*0*	**50**	**69**	**50**
Commelina diffusa	**67**	*17*	**89**	**70**
Leersia hexandra	**35**	*0*	**58**	**40**
Echinochloa colona	**71**	*22*	*27*	**90**
Bidens pilosa	*2*	**78**	**60**	*20*
Desmodium triflorum	13	**28**	**31**	*0*
Echinochloa oryzoides	*5*	**67**	**51**	*10*
Isachne globosa	*7*	**44**	**51**	*10*
Ludwigia adscendens	9	**33**	**20**	*0*
Oldenlandia diffusa	*4*	**56**	**51**	20
Fimbristylis aestivalis	*0*	**78**	**22**	*0*

Species richness on the bunds was at an average of 28.5 species per relevé (SD: 11.7, range: 0–56). One hundred and twenty species occurred with less than 1% constancy. The mean number of recorded species was significantly higher in the mountains than in the lowlands (Welch Two Sample t-Test, $t_{76} = 4.91$, $p < 0.001$), with 35.3 and 26.7 species per relevé, respectively. The total number of taxa recorded in the mountains was lower, as was the number of collected relevés (Fig. 3.1a). Besides, more species were recorded in the Philippines, though the mean number of species recorded per bund relevé was higher in Vietnam (Wilcoxon-Mann-Whitney Test, U = 1477, Z = -3.226, p = 0.001, r = 0.28). Species richness and sampling effort was lowest in the Mekong

region VN4. Most relevés were collected in PH2 while most species were recorded in PH1 and PH3.

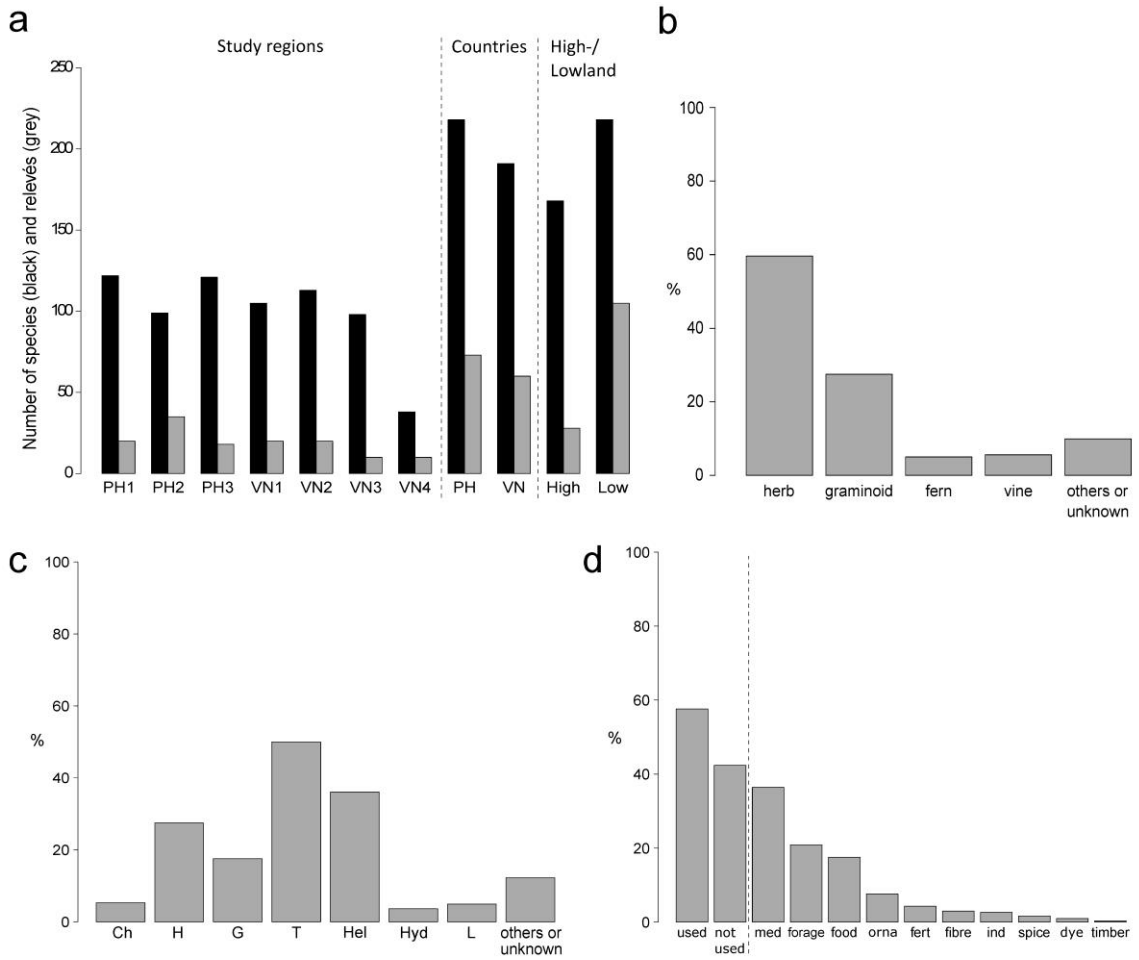

Fig. 3.1: The floristic diversity and composition on Southeast Asian rice field bunds was investigated from 2012 to 2015: (a) Numbers of species (black) and relevés (grey) in the different study regions, countries and altitudinal levels. Percentages of (b) plant growth forms and (c) plant life forms occurring on rice field bunds (Ch = chamaephytes, H = hemicryptophytes, G = geophytes, T = therophytes, Hel = helophytes, Hyd = hydrophytes, L = lianas/vines). (d) Percentages of useful plants encountered on the studied rice field bunds (med = medicine, orna = ornamental, fert = fertilizer, ind = industrial resource), multiple use possible (IUCN 2015; eFloras 2008).

The majority of species encountered were non-graminoid herbs (ca. 60%), whereas graminoids contributed to nearly 30% (Fig. 3.1b). Half of the species were therophytes, whereas hemicryptophytes and geophytes occurred in much lower percentages (28% and 18%, respectively) (Fig. 3.1c). Helophytes were represented in equal proportions by annuals and perennials and constituted 36% of the total species pool. Other lifeforms like chamaephytes, hydrophytes or woody lianas did not exceed 5%.

3.4.2 Classification of relevés and determination of diagnostic species

UPGMA classification of the bund vegetation revealed six clusters assignable to three groups (dendrogram see Appendix A.12). The differential species of the clusters and species occurring more than twice are listed in Table 3.3. The groups combine floristically and ecologically related bund communities, and differ amongst each other, apart from their species composition, mainly by their species diversity, geographical distribution, and related differences in climate, altitude, structural diversity and land use intensity (Table 3.1 and 3.4): **Lowland group A** consists of two relatively species-poor communities (A1 and A2), typically encountered in areas of intensive crop farming and rather low structural diversity, in the hot tropical regions of the Vietnamese and Philippine lowlands (VN4, PH1 and PH2). Both communities are characterized by *Eriochloa procera,* an annual or short-lived perennial grass, with the disturbance-tolerant grass *Paspalum conjugatum* and the herbs *Ludwigia hyssopifolia*, *Alternanthera sessilis*, *Oldenlandia corymbosa*, *Ludwigia octovalvis*, *Hyptis brevipes* and *Hydrolea zeylanica* frequently co-occurring (Appendix A.8). **Lowland group B** (with communities B3 and B4) occurred chiefly under subtropical conditions, in less homogeneous landscapes of rather intermediate land use intensity (VN1, VN2 and PH1). The species diversity was comparably high. Main diagnostic species were the fast-growing grasses *Panicum repens*, *Axonopus compressus* and *Hymenachne amplexicaulis* among common noxious rice weeds like *Alternanthera sessilis*, *Commelina diffusa*, *Kyllinga brevifolia*, *Leptochloa chinensis*, *Ludwigia hyssopifolia* etc. (Appendix A.9). **Mountain group C** contains two species-rich plant communities (C5 and C6) on bunds in the tropical and subtropical mountain regions (PH3 and VN3), characterized by heterogeneous landscapes and traditional farming systems with limited chemical input. Several species are diagnostic for this group: *Ageratum conyzoides*, *Digitaria ciliaris*, *Hypericum japonicum*, *Phyllanthus urinaria*, *Fimbristylis dichotoma*, *Oxalis corniculata*, *Arthraxon* spec., *Oenanthe javanica*, *Crassocephalum crepidioides*, *Digitaria violascens* and *Lindernia setulosa* (in order of frequency) (Appendix A.10).

Table 3.3: Synoptic table showing the differential species on Southeast Asian rice field bunds with their constancies (%) in the different clusters. Differential taxa (dark-grey bold = positively differentiating, light-grey italic = negatively differentiating, grey bold italic= positive-negatively differentiating) were identified with the algorithm of Tsiripidis et al. (2009).

ClusterID	**A1**	**A2**	**B3**	**B4**	**C5**	**C6**
Number of relevés	38	8	13	41	18	10
Positive differential species of A1						
Cyperus rotundus	**50**	*0*	23	12	*6*	*0*
Polytrias indica	**34**	13	*0*	*0*	*0*	*0*
Cleome rutidosperma	**26**	13	15	*2*	*0*	*0*
Brachiaria subquadripara	**24**	*0*	8	*0*	*0*	*0*
Melochia corchorifolia	**24**	13	8	*2*	*0*	*0*
Phyllanthus debilis	**24**	13	15	17	*0*	*0*
Positive differential species of B3						
Kyllinga nemoralis	*3*	*13*	**54**	*0*	*0*	*0*
Oldenlandia biflora	*3*	*0*	**54**	*0*	*0*	*0*
Ammannia baccifera	*3*	*0*	**46**	*0*	*0*	*0*
Ischaemum polystachyum	*3*	*13*	**46**	*2*	*0*	*0*
Brachiaria mutica	16	*13*	**46**	*2*	*0*	*0*
Basilicum polystachyon	*0*	*0*	**38**	*0*	*0*	*0*
Spermacoce laevis	*5*	13	**38**	*2*	*0*	*0*
Synedrella nodiflora	13	13	**38**	*7*	*6*	*0*
Euphorbia prostrata	13	13	**38**	*0*	*0*	*0*
Dentella repens	*3*	*0*	**31**	*2*	*0*	*0*
Cyathula prostrata	*0*	*0*	**23**	*0*	*0*	*0*
Persicaria barbata	*0*	*0*	**23**	*0*	*0*	*0*
Ludwigia perennis	*0*	13	**23**	*0*	*0*	*0*
Rottboellia cochinchinensis	*0*	*0*	**23**	2	*0*	*0*
Acmella uliginosa	*0*	*0*	**23**	2	6	*0*
Digitaria setigera	3	13	**23**	17	*0*	*0*
Amaranthus viridis	5	13	**23**	7	6	*0*
Positive differential species of B4						
Hydrocotyle sibthorpioides	*0*	*0*	*8*	**76**	*0*	*0*
Rotala rotundifolia	*0*	*0*	*0*	**63**	*0*	*0*
Marsilea minuta	*0*	*0*	*0*	**61**	*0*	*0*
Centipeda minima	*0*	*0*	*0*	**54**	*0*	*10*
Lindernia procumbens	*3*	*0*	*0*	**46**	*11*	*0*
Panicum auritum	*0*	*0*	*0*	**44**	*0*	*0*
Echinochloa crus-galli	16	13	15	**37**	*0*	*0*
Lemna aequinoctialis + minor	*0*	*0*	*0*	**32**	*0*	10
Gonostegia pentandra	*3*	*0*	8	**27**	*0*	*0*
Alternanthera philoxeroides	5	*0*	*0*	**22**	*0*	*0*
Pistia stratiotes	*0*	13	8	**22**	*0*	*0*
Murdannia spirata	*0*	*0*	*0*	**20**	*0*	*0*
Positive differential species of C5						
Cuphea carthagenensis	*0*	*0*	*0*	*0*	**100**	*0*
Fimbristylis aestivalis	*0*	*0*	*0*	***24***	**78**	*0*
Cyclosorus interruptus	*3*	*0*	*0*	*7*	**67**	*0*

Table 3.3: (continued)

ClusterID	A1	A2	B3	B4	C5	C6
Number of relevés	38	8	13	41	18	10
Equisetum ramosissimum ssp. *debile*	*0*	*0*	*0*	*0*	**67**	*0*
Gonostegia hirta	*5*	*13*	*8*	*0*	**67**	*20*
Imperata cylindrica	18	*13*	*8*	*5*	**67**	30
Paspalum scrobiculatum	*11*	*0*	*0*	*17*	**56**	*10*
Pycreus flavidus	*0*	*0*	*0*	*0*	**50**	*0*
Cardamine hirsuta	*0*	*0*	*0*	*0*	**39**	10
Apluda mutica	*0*	*0*	*0*	*0*	**22**	*0*
Galinsoga parviflora	*0*	*0*	*0*	*0*	**22**	10
Positive differential species of C6						
Rotala indica	*0*	*0*	*0*	*22*	*6*	**100**
Cyperus haspan	*0*	*0*	*0*	***32***	*11*	**90**
Hydrocotyle pseudoconferta	*0*	*0*	*0*	*0*	*0*	**80**
Murdannia nudiflora	*3*	*13*	*8*	*12*	*0*	**80**
Potentilla kleiniana	*0*	*0*	*0*	*0*	*0*	**80**
Pseudognaphalium hypoleucum	*0*	*0*	*0*	*0*	*6*	**70**
Plantago asiatica	*0*	*0*	*0*	*0*	*0*	**70**
Lamiaceae spec. (1)	*0*	*0*	*0*	*0*	*0*	**70**
Cyperus difformis	29	38	31	39	*17*	**70**
Juncus prismatocarpus	*0*	*0*	*0*	*7*	*0*	**60**
Setaria pumila	*0*	*0*	*0*	*0*	*0*	**60**
Pycreus sanguinolentus	*0*	*0*	*0*	*7*	*0*	**60**
Selaginella ciliaris	*0*	*0*	*0*	*0*	*0*	**50**
Desmodium spec.	*0*	*0*	*0*	*0*	*0*	**40**
Lobelia nummularia	*0*	*0*	*0*	*0*	*0*	**40**
Schoenoplectiella juncoides	*0*	*0*	*0*	*0*	*6*	**40**
Paspalum urvillei	*0*	*0*	*0*	*0*	*0*	**40**
Persicaria nepalensis	*0*	*0*	*0*	*0*	*0*	**30**
Ranunculus cantoniensis	*0*	*0*	*0*	*0*	*0*	**30**
Sagittaria trifolia	*0*	*0*	*0*	12	*0*	**30**
Differential species of higher-ranking groups						
Eriochloa procera	**24**	**63**	15	17	*0*	*0*
Panicum repens	*24*	*25*	**77**	**88**	*6*	*10*
Axonopus compressus	*5*	*13*	**54**	**61**	*0*	*0*
Hymenachne amplexicaulis	*0*	*0*	**31**	**20**	*0*	*0*
Ageratum conyzoides	*39*	*25*	62	41	**100**	**100**
Digitaria ciliaris	*21*	*25*	*23*	61	**67**	**100**
Hypericum japonicum	*0*	*0*	*0*	*7*	**67**	**100**
Phyllanthus urinaria	*21*	*25*	62	37	**83**	**70**
Fimbristylis dichotoma	*3*	*0*	*15*	*12*	**56**	**70**
Oxalis corniculata	*0*	*0*	*8*	17	**33**	**70**
Arthraxon spec.	*0*	*0*	*0*	*0*	**56**	**20**
Crassocephalum crepidioides	*0*	*0*	8	*0*	**22**	**40**
Oenanthe javanica	*0*	*0*	*0*	*2*	**33**	**30**

Table 3.3: (continued)

ClusterID	A1	A2	B3	B4	C5	C6
Number of relevés	38	8	13	41	18	10
Digitaria violascens	*0*	*0*	*0*	7	**39**	**20**
Lindernia setulosa	*0*	*0*	*0*	*0*	**33**	**20**
Differential species with at least 20% constancy						
Ludwigia hyssopifolia	**71**	**100**	**54**	**88**	**39**	*0*
Alternanthera sessilis	**79**	**50**	**100**	**98**	**50**	*10*
Paspalum conjugatum	**74**	**50**	**69**	**39**	**83**	*0*
Kyllinga brevifolia	*11*	**50**	**92**	**90**	**94**	**90**
Oldenlandia corymbosa	**29**	**50**	**54**	**51**	*0*	*0*
Ludwigia octovalvis	**34**	**38**	**54**	*10*	**78**	*0*
Hyptis brevipes	**32**	**25**	**38**	*0*	**28**	*0*
Leersia hexandra	*8*	**50**	**85**	**66**	*0*	**40**
Centella asiatica	*5*	*13*	**54**	**46**	**67**	**60**
Drymaria cordata	*0*	*0*	**31**	**39**	**50**	**60**
Commelina diffusa	58	*25*	**100**	**98**	*17*	**70**
Mazus pumilus	*0*	*0*	**23**	**32**	17	**40**
Leptochloa chinensis	34	**100**	**77**	**76**	*6*	*10*
Cynodon dactylon	**100**	*25*	**54**	**80**	*11*	*0*
Cyperus iria	**47**	25	**62**	**46**	*11*	40
Ipomoea aquatica	**34**	13	**38**	**27**	*0*	*0*
Eleusine indica	58	38	**85**	**63**	**94**	*20*
Lindernia anagallis	*0*	*0*	*0*	**76**	**50**	**50**
Cyperus pilosus	*3*	*0*	*0*	**27**	**50**	**30**
Sacciolepis indica	*0*	*0*	*0*	**32**	**39**	**30**
Rorippa indica	*0*	*13*	**46**	*7*	**72**	**40**
Oldenlandia diffusa	*8*	**50**	*0*	**44**	**56**	20
Mikania cordata	*0*	**25**	**31**	*0*	**33**	*0*
Hydrolea zeylanica	**26**	**25**	**23**	12	*0*	*0*
Paspalum distichum	32	*13*	*0*	**100**	44	**70**
Ludwigia prostrata	*0*	*0*	*0*	**83**	*0*	**60**
Persicaria minor	*0*	*0*	*0*	**44**	*17*	**80**
Persicaria hydropiper	*0*	*0*	*0*	**24**	*0*	**20**
Azolla pinnata	*0*	*0*	*0*	**20**	17	**20**
Echinochloa colona	**79**	63	54	*22*	*22*	**90**
Bidens pilosa	*3*	*0*	*8*	**63**	**78**	*20*
Echinochloa oryzoides	*5*	25	*8*	**51**	**67**	*10*
Isachne globosa	*3*	*0*	23	**56**	**44**	*10*
Colocasia esculenta	*0*	*0*	23	**32**	**56**	10
Desmodium triflorum	13	13	8	**34**	**28**	*0*
Ludwigia adscendens	13	*0*	*0*	**22**	**33**	*0*
Ischaemum rugosum	**45**	25	**54**	*10*	*0*	*0*
Cyanthillium cinereum	**42**	25	**54**	17	*6*	*0*
Ipomoea triloba	**21**	*0*	**23**	5	*0*	*0*
Pseudelephantopus spicatus	*3*	*13*	**54**	*0*	**39**	*0*
Euphorbia hirta	13	*0*	**31**	*5*	**50**	*0*

Table 3.3: (continued)

ClusterID	**A1**	**A2**	**B3**	**B4**	**C5**	**C6**
Number of relevés	38	8	13	41	18	10
Hyptis capitata	*0*	*0*	**23**	*0*	**28**	*0*
Ceratopteris thalictroides	*0*	**38**	8	**27**	*0*	*0*
Lindernia crustacea	11	**38**	15	**22**	11	*0*
Aeschynomene indica	*0*	**25**	**38**	5	*0*	20
Heliotropium indicum	13	**25**	**23**	7	*0*	*0*
Sphenoclea zeylanica	18	**25**	**23**	*2*	*0*	*0*
Scoparia dulcis	**24**	*0*	*0*	**24**	*0*	*0*
Frequent non-differential species						
Fimbristylis littoralis	82	100	77	80	78	100
Lindernia antipoda	42	100	92	49	78	70
Eclipta prostrata	79	50	77	98	89	60
Cultivated plants with more than two occurrences						
Oryza sativa	76	88	38	54	44	0
Phaseolus vulgaris	0	0	0	0	22	0
Other species with more than two occurrences						
Ammannia multiflora, Arundinella bengalensis, Chloris barbata, Chrysopogon aciculatus, Coccinia grandis, Commelina benghalensis, Corchorus aestuans, Corchorus olitorius, Cucumis debilis, Cyanthillium patulum, cf. *Cyclosorus* spec. (1)*, Cyperus compressus, Davallia denticulata, Emilia sonchifolia, Eragrostis unioloides, Erigeron floribundus, Fabaceae* spec. (2)*, Ipomoea obscura, Ischaemum barbatum, Lindernia rotundifolia, Lygodium microphyllum,* cf. *Malvastrum coromandelianum, Marsilea crenata, Mentha arvensis, Mimosa pudica, Phyllanthus virgatus, Physalis angulata, Pogonatherum crinitum, Polygonum plebeium, Sida alnifolia* var. *alnifolia, Solanum americanum, Sphaeranthus africanus, Spirodela polyrrhiza, Stellaria aquatica, Urena lobata,* Plantae indet. (10)						

Generally, a strong geographical differentiation of the vegetation is evident as most of the clusters occur largely in a particular region, although they may not be restricted to it (Table 3.4). Environmental conditions and cultivation methods vary between the six clusters that are ecologically best distinguished by the parameters elevation, mean annual temperature, pH, C/N ratio, geographic range, the number of crops per year, season, and species diversity (Table 3.4). The two clusters of a group always differed between each other in mean soil acidity, often also nutrient availability.

Table 3.4: The vegetation survey was designed to detect possible effects of environmental and other variables on the Southeast Asian bund vegetation. Important parameters characterizing the vegetation are summarized: mean annual temperature, pH (soil acidity), EC (electrical conductivity), C/N ratio, crops/year, herb cover, species richness, Shannon diversity and evenness are represented as means ± standard deviation.

Main cluster group	Lowland group A		Lowland group B		Mountain group C	
Cluster	A1	A2	B3	B4	C5	C6
Min. elevation [m a.s.l.]	6	4	8	0	780	725
Max. elevation [m a.s.l.]	80	40	290	34	1182	1390
Median elevation [m a.s.l.]	55	21	27	8	975	1231
Mean annual temperature [°C]	27.1	27.6 ± 0.2	27.2 ± 0.1	24.6 ± 0.1	20.2 ± 0.3	19.4 ± 0.5
pH	6.14 ± 0.10	5.68 ± 0.23	6.50 ± 0.08	5.72 ± 0.10	5.44 ± 0.09	4.71 ± 0.11
EC [µS/cm]	146 ± 20	385 ± 63	367 ± 52	113 ± 13	427 ± 44	241 ± 18
C/N ratio	13.1 ± 0.4	11.4 ± 0.4	11.0 ± 0.3	9.1 ± 0.3	11.0 ± 0.9	11.1 ± 0.2
No. of crops [y^{-1}]	2.1 ± 0.1	2.4 ± 0.2	2	2	1	1
Herb cover [%]	64 ± 5	47 ± 13	71 ± 4	75 ± 2	40 ± 5	94 ± 2
Species richness (10 m^2)	21 ± 1	20 ± 4	33 ± 3	35 ± 1	35 ± 2	36 ± 2
Shannon diversity	2.0 ± 0.1	2.0 ± 0.2	2.3 ± 0.1	2.5 ± 0.1	2.6 ± 0.1	2.7 ± 0.1
Evenness	0.69 ± 0.02	0.70 ± 0.06	0.67 ± 0.03	0.72 ± 0.02	0.73 ± 0.02	0.77 ± 0.01
Season [no. of relevés]	wet [11], dry [27]	wet [3], dry [5]	dry [13]	wet [40], dry [1]	wet [18]	wet [10]
Region [no. of relevés]	PH1 [2], PH2 [34],VN4 [2]	PH1 [4], PH2 [1],VN4 [3]	PH1 [13]	PH1 [1],VN1 [20],VN2 [20]	PH3 [18]	VN3 [10]
Country [no. of relevés]	PH [36],VN [2]	PH [5],VN [3]	PH [13]	PH [1],VN [40]	PH [18]	VN [10]
Soil texture	Sandy loam - Silty clay	Silt - Silty clay	Sandy loam - Loam	Sandy loam - Silty clay	Sandy loam - Silt loam	Sandy loam - Silt loam

3.4.3 Indirect gradient analysis

The NMDS results (final stress: 0.163) support the classification in clearly arranging pairs of clusters in three distinct groups along axes 1 and 2, with sites of mountain group C scoring on the lower right and those of lowland groups A and B on the center left and top, respectively (Fig. 3.2a). Relationships between plant community composition and observed environmental variables were found to be best reflected in Fig. 3.2b and Table 3.5. The first axis, representing the principal floristic gradient, showed high correlation with annual mean temperature (and elevation), species diversity, C/N ratio and number of crops per year. Again, groups A to C were arranged from left to right. Previously grouped clusters were pulled apart along a gradient of soil acidity (pH) represented by NMDS axis 3. Inferring from the small overlap of the area scores and from the fact that most clusters occurred largely in a particular study area the geographic position also played an important role. The Philippine sites, generally associated with less acidic soils, scored rather on the bottom left whereas the more acidic Vietnamese sites scored on the top right. Species richness (S), evenness (J) and Shannon index (H) indicate that clusters C5 and C6 comprised the highest species diversity, while at the same time the number of recorded species correlated negatively with crops per year. Generally, mean annual temperature (MeanTemp) and species richness showed the strongest correlation with NMDS axis 1, while soil acidity and evenness correlate significantly with both axes (1 and 3).

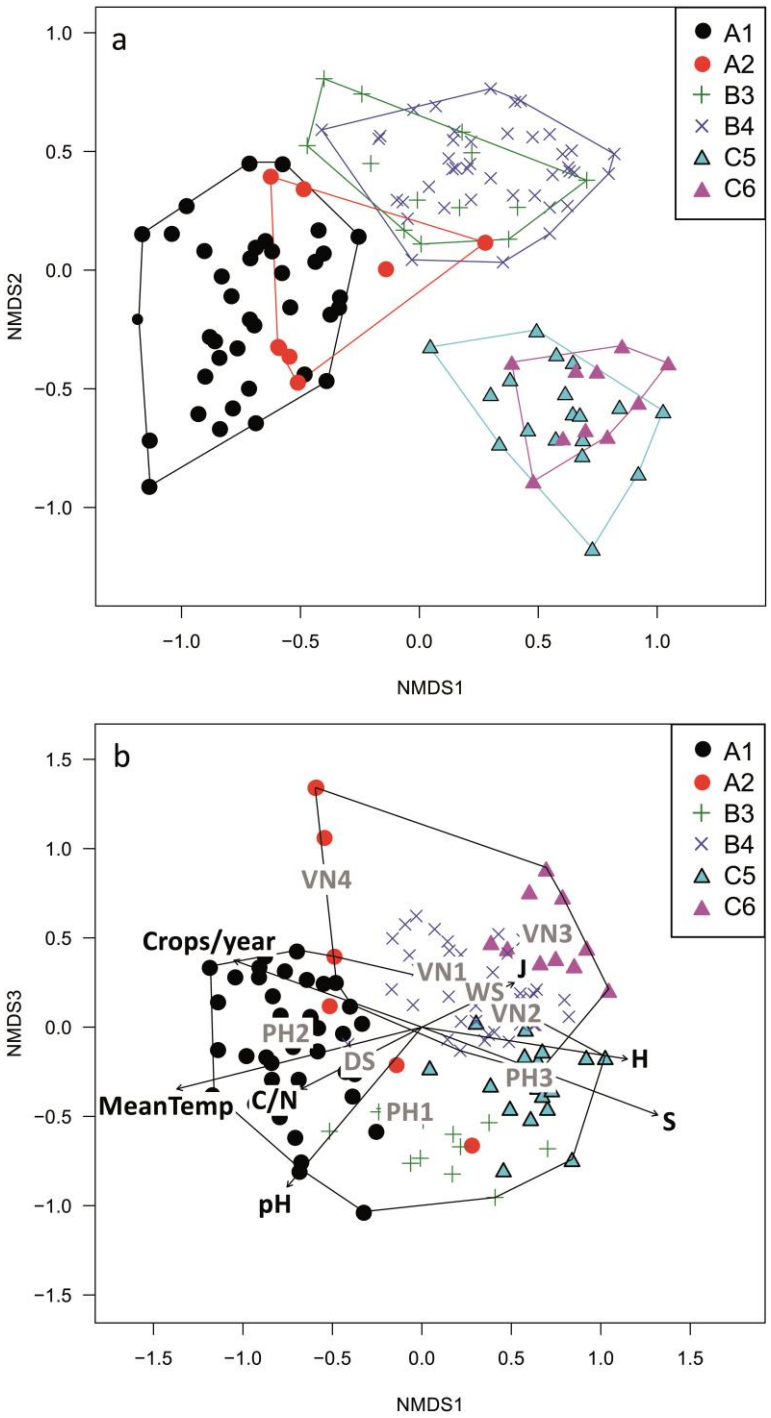

Fig. 3.2: Site scores of the NMDS ordination are shown along axes 1 and 2 (a), and axes 1 and 3 (b). Symbols indicate the different clusters (numbered as in the text and Tables 3 and 4). Envelopes in (a) indicate the clusters, in (b) the two countries (top = VN, bottom = PH). Numerical environmental variables that correlate significantly (p <0.05) with NMDS axes are indicated as arrows, categorical variables (incl. regions) as grey centroids. (DS = dry season, H = Shannon diversity, J = evenness, MeanTemp = mean annual temperature 2001–06, S = species richness, WS = wet season.)

Table 3.5: NMDS ordination was performed to visualize variation in plant community composition and the determinants. The table lists environmental variables (abbreviations used in Fig. 3.2b are given in brackets) that were fit a posteriori onto the ordination, their correlation with the NMDS axes 1 and 3, the goodness of fit (R^2) and the significance of each correlation (p; ** and *** mean significant at 1 and 0.1% levels, respectively). Centroids of each level of a categorical variable are listed separately before R^2 and p of the particular category is given.

	NMDS1	NMDS3	R^2	p	
Elevation a.s.l.	1.000	-0.015	0.313	0.001	***
Soil moisture	-0.498	0.867	0.016	0.408	
Soil acidity (pH)	-0.645	-0.764	0.391	0.001	***
Electrical conductivity (EC)	0.511	-0.859	0.020	0.308	
C/N ratio	-0.888	-0.460	0.165	0.001	***
Humus content	0.368	-0.930	0.016	0.427	
Mean annual temperature (MeanTemp)	-0.970	-0.242	0.570	0.001	***
Crops/year	-0.941	0.339	0.358	0.001	***
Herb cover	-0.041	0.999	0.013	0.476	
Species richness (S)	0.938	-0.347	0.566	0.001	***
Shannon diversity (H)	0.989	-0.151	0.386	0.001	***
Evenness (J)	0.900	0.437	0.094	0.004	**
Region_PH1	-0.081	-0.484			
Region_PH2	-0.734	-0.034			
Region_PH3	0.590	-0.289			
Region_VN1	0.127	0.317			
Region_VN2	0.487	0.104			
Region_VN3	0.719	0.503			
Region_VN4	-0.521	0.822			
Region			0.747	0.001	***
Landscape heterogeneity_High	0.072	-0.066			
Landscape heterogeneity_Low	0.041	0.101			
Landscape heterogeneity			0.014	0.173	
Season_Dry (DS)	-0.450	-0.229			
Season_Wet (WS)	0.376	0.169			
Season			0.386	0.001	***

3.4.4 Description of plant communities

Lowland group A (Appendix A.8, rel. 1–46)

Main diagnostic species: *Eriochloa procera*

A1: *Cynodon dactylon-Cyperus rotundus* community (rel. 1–38)

This community type was mainly found in the hot tropical lowlands of Nueva Ecija (PH2), but also in Laguna (PH1) and the Mekong Delta (VN4). Intensity of the local agricultural production is rather high and structural diversity at a low to medium level. The bunds were moderately vegetated and consisted of slightly acid soils with relatively

low nutrient levels. Species diversity in this community was rather low (mean number: 21, SD: 1). The cosmopolitan graminoids *Cynodon dactylon* and *Cyperus rotundus*, both very trampling-resistant, were most characteristic, besides the grasses *Polytrias indica* and *Brachiaria subquadripara*. *Cleome rutidosperma*, *Melochia corchorifolia* and *Phyllanthus debilis* were the most typical dicot weeds.

A2: *Leptochloa chinensis-Leersia hexandra* community (rel. 39–46)

The most species-poor community occurred in the same hot tropical lowland regions, but was restricted to sites with very intensive crop farming and consequently increased disturbance and damage of the bund vegetation. The soils were moderately acid and the nutrient availability increased, and the cover of the herb layer and the species diversity were low (mean number: 20, SD: 4). The community shares some diagnostic species with community A1 and is rather poorly distinguished by some common rice field weeds, i.e. *Leptochloa chinensis*, *Leersia hexandra*, *Oldenlandia diffusa*, *Kyllinga brevifolia*, *Ceratopteris thalictroides*, *Lindernia crustacea*, *Heliotropium indicum* and *Sphenoclea zeylanica*.

Lowland group B (Appendix A.9, rel. 47–100)

Main diagnostic species: *Panicum repens*, *Axonopus compressus*, *Hymenachne amplexicaulis*

B3: *Kyllinga nemoralis-Ischaemum polystachyum* community (rel. 47–59)

This community type was only found in the Laguna Province (PH1) located in the southern tropical lowlands of Luzon Island, on slightly acid soils with good supply of micronutrients and nitrogen. While species numbers were relatively high (mean: 33, SD: 3), species abundances were unbalanced as indicated by the lowest evenness of all bund communities. Main diagnostic graminoids were the perennial white water sedge *Kyllinga nemoralis* and the grasses *Ischaemum polystachyum* and *Brachiaria mutica*, further the annual grasses *Rottboellia cochinchinensis* and *Digitaria setigera*. Most characteristic dicot herbs are annual, i.e. *Acmella uliginosa*, *Amaranthus viridis*, *Ammannia baccifera*, *Basilicum polystachyon*, *Euphorbia prostrata*, *Ludwigia perennis*, *Spermacoce laevis* and *Synedrella nodiflora*, whereas the rhizomatous helophyte *Persicaria barbata* is an obligate perennial. *Oldenlandia biflora*, *Cyathula prostrata* and *Dentella repens* adjust their life span to given conditions.

B4: *Paspalum distichum-Hydrocotyle sibthorpioides* community (rel. 60–100)

This community represents lowland bund vegetation, mainly along the Red River, in the subtropical North of Vietnam. Hai Duong (VN1) and Vinh Phuc (VN2) are located close to each other in terms of geography and floristic composition. Acidity of the soils ranged between strongly acidic to neutral, though the bunds in Vinh Phuc had on average lower pH levels. All soils showed favorable C/N ratios and rather low salt contents. Bunds of both regions had a relatively high species diversity (mean number: 35, SD: 1), including the differential species *Hydrocotyle sibthorpioides*, *Rotala rotundifolia*, *Marsilea minuta*, *Centipeda minima*, *Lindernia procumbens*, *Panicum auritum*, *Echinochloa crus-galli*, *Lemna aequinoctialis* + *minor*, *Gonostegia pentandra*, *Pistia stratiotes*, *Alternanthera philoxeroides* and *Murdannia spirata*.

Mountain group C (Appendix A.10, rel. 101–128)

Main diagnostic species: *Ageratum conyzoides*, *Digitaria ciliaris*, *Hypericum japonicum*, *Phyllanthus urinaria*, *Fimbristylis dichotoma*, *Oxalis corniculata*, *Arthraxon* spec., *Oenanthe javanica*, *Crassocephalum crepidioides*, *Digitaria violascens*, *Lindernia setulosa*

C5: *Cuphea carthagenensis-Fimbristylis aestivalis* community (rel. 101–118)

This community type occurs in a tropical mountain climate on the bunds of the Philippine rice terraces in Ifugao (PH3). The bunds are sometimes shallow and contain big rocks used during the construction of terrace walls. Their soils are rather coarse, strongly acidic and contained the highest salt loads measured. The terraces were managed in traditional manner: input of chemicals for fertilization and inhibition of weed growth is reduced, but manual methods of weed control are intensified. The species diversity was high (mean number: 35, SD: 2), although the herb cover was low. The community was differentiated by *Cuphea carthagenensis*, *Fimbristylis aestivalis*, *Cyclosorus interruptus*, *Equisetum ramosissimum* ssp. *debile*, *Gonostegia hirta*, *Imperata cylindrica*, *Paspalum scrobiculatum*, *Pycreus flavidus*, *Cardamine hirsuta*, *Apluda mutica* and *Galinsoga parviflora* (in order of frequency).

C6: *Rotala indica-Cyperus haspan* community (rel. 119–128)

The bunds with the highest species diversity (mean number: 36, SD: 2) were found lining the rice terraces of Lao Cai (VN3). The soils of the heterogeneous mountain landscape in the Vietnamese subtropics are very strongly acidic, rather coarse and, like in Ifugao, sometimes shallow because big stones are integrated in the terrace walls. Local traditional rice cultivation is without use of chemicals, but involves intensive surveillance and manual labor. The bunds were nevertheless heavily vegetated by the time of sampling and species were more evenly distributed than in any other community type. The main diagnostic species were *Rotala indica*, *Cyperus haspan*, *Hydrocotyle pseudoconferta*, *Murdannia nudiflora*, *Potentilla kleiniana*, *Pseudognaphalium hypoleucum*, *Plantago asiatica*, cf. *Mosla cavaleriei*, *Cyperus difformis*, *Juncus prismatocarpus*, *Setaria pumila*, *Pycreus sanguinolentus*, *Selaginella ciliaris*, *Desmodium* spec., *Lobelia nummularia*, *Schoenoplectiella juncoides*, *Paspalum urvillei*, *Persicaria nepalensis*, *Ranunculus cantoniensis* and *Sagittaria trifolia* (in order of frequency).

3.5 Discussion

3.5.1 Plant diversity and composition of bunds compared to paddies

Rice agroecosystems are man-made wetlands. They consist chiefly of paddies where rice is cultivated, accompanied by adapted weed communities. Though often fragmentary and comparatively species-poor (Miyawaki 1988), paddies host a variety of specialized species, many of which are globally rare (IUCN 2015; Nowak et al. 2015; Fried et al. 2017). The bunds subdivide these landscapes, forming a network of linear elements with much higher plant diversity and cover. Our results from bunds (plot size 10 m²) and adjacent paddies (Fried et al. 2017) show that mean species richness was about four times higher on bunds, despite smaller plot size, and also the herb cover was generally much higher (Appendix A.13). The two habitat types shared a total of 102 species (Appendix A.5), only ten species were found exclusively in paddies (e.g. *Ammannia coccinea*, *Ammannia microcarpa*, *Characeae* spec., *Eriocaulon cinereum*, *Limnophila aromatica*, *Potamogeton distinctus*, *Rotala mexicana* and *Schoenoplectiella mucronata*), whereas the highest proportion (199 species or 63%) was recorded only on bunds. This indicates that bunds, complementary to paddies, are an important source,

refuge and corridor of plants in rice agroecosystems. Moreover, they possess a distinct flora and vegetation. Similar results confirming the higher species diversity on bunds in comparison to paddies are also known from Sri Lanka (Bambaradeniya et al. 1998), China (Nemoto & Otsuka 2014), Java (Kumalasari & Bergmeier 2014) and Japan (Fukamachi et al. 2005). In general, the paddy habitat is more exclusive, selective, and homogenized through flooding, weed control, seeding and/or seed contamination, resulting in a comparatively species-poor flora. The bunds are likely to play a key role if the Southeast Asian agrobiodiversity is to be preserved.

The life form composition on bunds shows major similarities to the paddy vegetation of southern Europe, Japan and Southeast Asia as semi-aquatic conditions and rigorous weeding practices favor an annual, often amphibious life form (Bolòs & Masclans 1955; Miyawaki 1960; Fried et al. 2017). High percentages of helophytes and species that are capable of adjusting their life cycle in response to their environment support the close floristic relationship of the bund communities with the amphibious vegetation of paddies and natural wetlands. In contrast, hydrophytes are absent, except for an occasional miniature puddle, because bunds function as water boundaries and pathways. Additionally, trampling favors the emergence of weeds with pre-adapted traits like flexible, horizontally branching stems, narrow leaves etc., qualifying grasses and other graminoids as the most resistant and resilient growth form (e.g. Yorks et al. 1997; Carni & Mucina 1998; Hill & Pickering 2009).

3.5.2 Spatial differentiation in bund vegetation compared to paddies

Relevés of both paddies and bunds reveal higher mean species richness and species turnover in the rice terrace landscapes, probably as a result of increased structural diversity (c.f. Fried et al. 2017). Mountainous regions within the humid tropics often support higher biodiversity as a result of the combined effects of suitable climatic conditions and high geodiversity (Barthlott et al. 2005). In agrarian landscapes, differences in land use practices and intensity probably add to such effects (Fried et al., in press, chapter 4). Differences in species richness between the countries are less prominent (Appendix A.13). The lowest number of species was found on bunds in the Mekong Delta (VN4), probably caused by a strong negative impact of intensive agricultural production. In a similar number of relevés in Lao Cai (VN3), 60 more

species were found. The unfavorable combination of high land use intensity and low structural diversity could also explain the low species diversity in Nueva Ecija (PH2).

On the community level, the geographical differentiation is much more pronounced on bunds than in paddies (c.f. Fried et al. 2017). This might be caused by several factors: (1) different methods and lower intensity of weed control, (2) higher species numbers, (3) more locally restricted anthropogenic dispersal due to lower seed contamination rates during harvest and planting, and (4) less hydrophytes or, in other words, a higher share of species that are obligate terrestrial for at least part of their life cycle and/or do not possess hydrochorous propagules. Santamaría (2002) explained in detail why aquatic plants generally show broader distributional ranges and lower taxonomic differentiation than their terrestrial counterparts. The local methods, intensities and consequences of weed control are discussed in chapter 3.5.5.

3.5.3 Rare and endangered plants in bunds of rice fields

The species composition on Vietnamese and Philippine rice field bunds is characterized by high abundances of graminoids and *Asteraceae*, *Linderniaceae*, *Lythraceae*, *Onagraceae* and *Rubiaceae* species. Several genera (e.g. *Ammannia*, *Brachiaria*, *Cyperus*, *Echinochloa*, *Eichhornia*, *Eleocharis*, *Hydrocotyle*, *Leersia*, *Ludwigia*, *Oryza*, *Paspalidium*, *Paspalum*, *Pycreus*, *Sagittaria*, *Schoenoplectiella*, *Scirpus* and *Scleria*) comprise vicarious species that are linked to eutrophic muddy environments in the Tropics (Deil 2005). Many notorious rice weeds have been found, but also taxa that are uncommon or rare in the study area, e.g. *Ammannia multiflora, Cyperus compactus, C. digitatus, C. distans, C. procerus, C. tenuispica*, *Dentella repens*, *Eleocharis congesta*, *Lindernia ciliata*, *L. hyssopoides*, *L. nummulariifolia*, *L. rotundifolia*, *Murdannia spirata*, *Rotala ramosior*, *R. rosea and R. rotundifolia*. Many more appear to be declining globally (IUCN 2015) and might become an issue for nature conservation. In total, 94 IUCN red listed species (yet 93 of which "Least concern") were recorded highlighting the need for intensified research on the local and regional species diversity and distribution. Several are listed in Japan as near threatened (*Leersia hexandra*, *Salvia plebeia*), vulnerable (*Azolla pinnata*, *Fimbristylis dichotoma*), endangered (*Pseudognaphalium hypoleucum*, *Rotala rosea*), critically endangered (*Marsilea crenata*, *Torenia concolor*) or even extinct (*Ophioglossum nudicaule*), while data on some more is deficient (Biodiversity Center of Japan, Ministry of Environment 2013).

Knowledge on ecosystem functions that the above-mentioned taxa provide for the local rice landscapes is scarce, which makes the conservation of these species and the preservation of their habitat conditions even more urgent. Interestingly, 176 of the recorded species are known to be used as medicine, food, spice, forage, fiber, ornamental plant, dye, or as an industrial resource, with some of the species being useful for multiple purposes (Fig. 3.1d, Appendix A.5) (eFloras 2008; IUCN 2015).

3.5.4 Community composition and environmental conditions

The bunds harbor therophyte-rich ruderal wetland vegetation which involves species of various phytosociological classes: *Oryzetea sativae*, *Stellarietea mediae*, *Polygono-Poetea annuae*, *Bidentetea tripartitae*, *Phragmito-Magno-Caricetea* and *Lemnetea*. Unlike in the paddies of the area, hydrophytes of the *Potamogetonetea* and *Charetea fragilis* were not represented (cf. Fried et al. 2017). The floristic inventory of bund communities shows the strongest relationship to the *Oryzetea sativae*. But frequent occurrences of species like *Axonopus compressus*, *Cynodon dactylon*, *Digitaria ciliaris*, *Eleusine indica*, *Paspalum conjugatum* indicate as well strong linkages to communities of trampled grassy habitats around the world, e.g. in Europe within the *Eragrostietalia*, or in Korea and Japan within the *Plantaginetalia asiaticae* Miyawaki 1964 (c.f. Mucina et al. 1991, 2016). In fact, paddies and (trampled) bunds are both characterized by heavy disturbance and, as a consequence of soil compaction and/or flooding, decreased soil aeration. On the other hand, many character species of trampled habitats from the temperate to subtropical regions of East Asia are missing. Besides, similarities with ephemeral freshwater wetlands of temperate to tropical regions around the world (c.f. Deil 2005) or segetal plant communities, e.g. the *Phyllanthus urinaria-Lindernia crustacea* association in Japan (Miyawaki 1969) or the West African *Ipomoeo eriocarpa*e-*Commelinetalia benghalensis* Wittig et al. 2011 of highly fertilized, humid soils in gardens and house fields (Wittig et al. 2011), exist. We conclude that the bund vegetation represents a mosaic or fragment complex of wet and dry segetal communities (*Oryzetea sativae* and *Stellarietea mediae*), interconnected with community fragments of trampled habitats (*Eragrostietalia*, *Plantaginetalia asiaticae*).

Amongst the climatic factors, the mean annual temperature was identified as an important discriminating variable for the differentiation of bund communities. Species composition changes with increasing elevation and distance from the equator, and

genera appear that are common in temperate regions, e.g. *Cardamine*, *Hypericum*, *Plantago* or *Potentilla*. Temperature triggers germination, emergence and growth rate of rice weeds differently (Smith, Jr. 1983), and studies from Indonesia (Kumalasari 2014), Tajikistan (Nowak et al. 2013), Nepal (Nowak et al. 2016) and the study area (Fried et al. 2017) have documented an influence of elevation or temperature on the community composition of rice weeds.

Seasonal patterns probably intensified differences between communities of Lowland group B as the species composition of B4 (including some hydrophytes) indicates wetter conditions, although hardly any variation of the water regime was observed. Community composition in tropical rice fields can change with the seasons if water availability is limited (cf. Kumalasari 2014) and also effects of the soil moisture on the weed flora of bunds in Sri Lanka are documented (Bambaradeniya et al. 1998). However, a correlation of soil moisture with community composition was neither found on bunds nor in adjacent paddies (c.f. Fried et al. 2017).

Our results also suggest a strong relation of the weed composition of bunds with the C/N ratio and the soil acidity. Soil pH is an important chemical property as it influences the availability of nutrients to plants (Fageria et al. 2011). Acidity in submerged soils causes denitrification, and thus, impedes the uptake of nitrogen (De Datta 1981; Blume et al. 2016). High levels of water saturation must also be expected in the bunds as they were only slightly elevated above the water table in predominantly flooded landscapes. Consequently, nitrogen availability might be reduced particularly in the mountain bunds, despite moderate C/N ratios, due to the general increase in soil acidity. Did low nitrogen availability enhance the local species diversity or influence the community composition as it does in other agroecosystems (e.g. Pyšek & Lepš 1991; Hyvönen & Salonen 2002)? Unfortunately, other comparable studies on fertility levels or chemical composition and their effects on the bund vegetation are not known to us. However, soil fertility showed major effects on the weed composition of paddies in Nepal (Nowak et al. 2016), whereas neither nutrients nor pH showed strong effects in Java (Kumalasari 2014) and Tajikistan (Nowak et al. 2013). Besides, the occurrence of a particular community might also be determined by the grain-size of the soils because vegetation clusters B3, C5 and C6 occurred only on rather sandy-silty soils with low clay content (5–18%), whereas others comprised a wide range of textural classes from sandy loam to silty clay. Relations between soil, management and vegetation could be disentangled

more profoundly with the inclusion of soil measurements into future vegetation analyses.

The number of crops per year and the land use intensity increase along the principal floristic gradient from the traditional highland farming systems to the intensive lowland production sites, while at the same time a clear negative correlation with a gradient of species diversity was observable (Fig. 3.2b). Variation in rice weed species richness at the community level was already related to cultivation intensity in adjacent paddies (Fried et al. 2017) and is also a main discrimination factor for Nepalese and Thai rice phytocoenoses (Nowak et al. 2015, 2016). Ongoing studies aim to quantify also the influence of landscape heterogeneity on the species diversity on different spatial scales (Fried et al., in press, chapter 4).

3.5.5 Weed control and cultivation methods

Different weed management techniques can change the floristic composition of rice fields and their bunds (e.g. IRRI 1983; Otsuka et al. 2006; Kumalasari 2014; Pinke et al. 2014). Bund weeds in the study area are mostly controlled by cutting, hand weeding, and herbicide application (Appendix A.11). Sometimes water buffalos graze on the bunds in the fallow period, but seldom during the period of rice cultivation for fear of crop loss. However, removed plant biomass might be used as a source of forage and other purposes (eFloras 2008; IUCN 2015). Mulching is very uncommon and was only observed in Ifugao and the Red River Delta. Varying land use habits on bunds correspond to observations from Java, Indonesia (Kumalasari 2014). As in Java, differences in weed control were most pronounced between upland and lowland regions. The traditional highland farming systems are characterized by low to zero input of synthetic herbicides (and fertilizers) and intensive manual labor. Removal of all bund weeds and the uppermost soil layer prior to the transplanting of rice seedlings is typically practiced by farmers in the mountains. In Ifugao, this practice is repeated up to four times during one crop cycle, whereas intensive surveillance and frequent hand weeding is especially common in Lao Cai (Appendix A.11). Moreover, the mountain climate allows for only one crop cycle per year, whereas two harvests are possible in irrigated lowland fields. Such characteristics and more, e.g. the use of traditional upland rice cultivars, are also known from other mountainous (rice) agroecosystems (De Datta 1981; Roder 1997; Roder et al. 1997; Galinato et al. 1999; Husson et al. 2001; Doanh &

Tuan 2004; Fukamachi et al. 2005; Paudel 2011; GRiSP 2013). The most intensive rice production was observed in the Mekong delta in Southern Vietnam, with three crop cycles per year, vast monoculture areas and high chemical input (also on bunds), leading to a severely depauperate flora.

3.6 Conclusion

Our records of Philippine and Vietnamese rice field bunds offer new insights into the composition and functioning of Asian rice cultivation landscapes. Bunds add various beneficial services to these valuable agroecosystems and they support a mosaic of specialized weed communities comprising many useful plants, sometimes even rare and declining on a global scale (IUCN 2015). The composition of communities gives information on environmental and biogeographical conditions, and is probably the best applicable and most reliable indicator of management intensity. In future, ditches and the rice terrace walls in exemplified mountainous regions are to be studied to complement our knowledge on local rice cultivation landscapes of Southeast Asia.

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Chapter 4:

Vascular plant species diversity in Southeast Asian rice ecosystems is determined by climate and soil conditions as well as the proximity of non-paddy habitats

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Abstract

Rice ecosystems vary greatly in climate, edaphic conditions, landscape heterogeneity, agricultural management and biodiversity. However, ongoing land use intensification and conversion to large-scale monoculture are threatening this diversity. We analyzed how rice-growing regions in Southeast Asia differ in diversity and composition of vascular plants in paddy rice ecosystems, and how the local and regional biodiversity of these plants is determined by variations in abiotic conditions, habitat type (paddy vs. bunds) and the proximity of non-paddy habitats. The vegetation of paddies and their bunds was surveyed in seven important rice production regions located in highlands and lowlands of Vietnam and the Philippines. Within the regions we sampled 67 pairs of study sites comprising a total of 122 paddies and 134 bunds. We identified major drivers of field-level weed diversity (alpha diversity) separately for bunds and paddies. Species turnovers (beta diversity) across sampling sites, between paddies and their bunds, and between regions were visualized using the Bray-Curtis coefficient of dissimilarity and DCA ordinations. Species richness on bunds was mainly influenced by the proximity of non-paddy habitats, mean annual temperature and soil acidity. Soil moisture was the decisive factor for the variation in paddy weed richness. In both habitat types, Shannon diversity and the number of insect-pollinated plants showed patterns similar to species richness. Regional differences in plot species richness were stronger on bunds than in paddies. Species turnover was high among habitat types and between upland and lowland regions. Future ecological engineering approaches can build on our findings to promote pollination services more efficiently in Southeast Asian rice landscapes.

4.1 Introduction

The world's population is predicted to reach 9.8 billion in 2050 (United Nations, 2017). Population growth, changes in consumption habits and augmented bioenergy use are likely to increase the global demand for agricultural products during the coming decades (Foley et al. 2011; Alexandratos & Bruinsma 2012; Martin & Sauerborn 2013). In Southeast Asia, about 32% of the terrestrial surface is already covered by agricultural land, ca. 28% is used to produce crops (FAO 2020). Rice is the most important food crop and main source of income in rural areas (GRiSP 2013). In 2018, 50 million ha were cultivated with rice in Southeast Asia (FAO 2020). Further agricultural expansion is at the expense of valuable natural and semi-natural habitats and associated organisms, and conventional land use intensification dramatically threatens farmland biodiversity (Foley et al. 2011; Cunningham et al. 2013; Newbold et al. 2015; Kehoe et al. 2017; Tilman et al. 2017). Agrobiodiversity plays a crucial role in maintaining essential ecosystem functions and services in agroecosystems like pest control, crop pollination, maintenance of soil fertility and water quality, erosion control, aesthetic and cultural values, provision of food, fodder, biofuels and fibers etc. (Altieri 1999; Martin & Sauerborn 2013). In general, higher plant species richness augments the spectrum of resources like nectar, pollen and habitats, and probably leads to a higher resilience against disturbances in agroecosystems. But if intensification continues over the next few decades as predicted, the global biodiversity value of agricultural lands will be substantially reduced (Egli et al. 2018).

Wild rice domestication began probably about 9,000 years ago and rice is now grown in irrigated paddies, or in rainfed lowland, rainfed upland and flood-prone ecosystems (Khush 1997). Paddy rice production systems consist of three main habitat types (Bambaradeniya & Amerasinghe 2003): the paddy (or field proper), the bund (levee) and the ditch (water supply canal). Together these habitat types form a mosaic of potentially high ecological, economical and socio-cultural value (GRiSP 2013). Paddies have mostly small local plant species pools (Miyawaki 1960), often reduced by weed control, whereas the vegetation on bunds is usually more abundant and speciose (Fried et al. 2018). Both habitat types host a variety of globally rare species (IUCN 2015; Nowak et al. 2015; Fried et al. 2017, 2018). In total, more than 1,800 plant species associated with rice cultivation were listed for South and Southeast Asia alone (Moody 1989). How this enormous plant diversity varies along environmental and spatial

gradients and which drivers cause species loss is not well understood. The drivers of the Southeast Asian rice weed diversity are scale-dependent due to complex, multi-levelled agro-ecological patterns and processes. Despite recent research on the species composition in South and Southeast Asian rice weed communities (Kumalasari 2014; Nowak et al. 2015, 2016; Fried et al. 2017, 2018), the factors underlying species diversity across habitats and regions remain to be determined. Besides climate, altitude, edaphic conditions and agricultural management, the surrounding landscape (e.g. the proximity of non-paddy habitats) may turn out to be a decisive factor for alpha, beta and gamma plant diversity in rice production systems. Lately, several studies examined the effects of the surrounding landscape on the plant diversity of agricultural areas, mainly in the Mediterranean (e.g. José-María et al. 2010; Armengot et al. 2011; Bassa et al. 2011) or temperate regions (e.g. Gabriel et al. 2005; Roschewitz et al. 2005; Poggio et al. 2013). Similar studies from tropical or subtropical rice fields are scarce and are inconclusive with respect to the effects of the proximity of non-crop habitats on weed diversity (Kumalasari 2014; Zhou et al. 2018). In this study, we analyze how local and regional-scale factors determine vascular plant diversity in tropical paddy rice agroecosystems. We sampled plant species in seven regions of Southeast Asia and covered three spatial levels: plots, landscapes and regions (in order of increasing area). We addressed the following questions: (a) What are the abiotic conditions and surrounding landscapes in the local paddy rice agroecosystems and what is their relative importance for vascular plants? (b) How and to which extent do plant diversity and composition differ within a region, between the paddies and their bunds, and across regions?

4.2 Methods

4.2.1 Study regions and experimental design

Our study regions, scattered over extensive areas in Southeast Asia, encompass considerable variation in climate, landscape heterogeneity, edaphic conditions, agricultural management and biodiversity. As described in chapter 1.5.1, we surveyed four study regions in Vietnam (VN1–4) and three in the Philippines (PH1–3), each covering 15 × 15 km (Fig. 1.7, Table 1.1).

Rice weed management and cultivation practices differ most strongly between lowland and upland regions rather than between countries (De Datta 1981; GRiSP 2013; Fried et al. 2017, 2018): rice is usually harvested twice a year in lowland regions, whereas the mountain climate allows for only one crop cycle per year. Intensive manual labor, the use of traditional upland rice cultivars and reduced or zero input of synthetic herbicides and fertilizers are further characteristics of the traditional upland rice farming systems in Ifugao (PH3) and Lao Cai (VN3). Besides, weeds and the uppermost soil layer are typically removed from the upland bunds prior to the transplanting of rice seedlings, and the use of water buffalos for puddling and harrowing of paddies is still common. In contrast, lowland farmers mostly use machinery and apply synthetic products for pest control and fertilization. Particularly Tien Gang (VN4) is characterized by high chemical input, vast monoculture areas and three crop cycles per year. In Laguna (PH1), bund weeds are subject to frequent cutting, but herbicides are used less than in other lowland regions. For further details on land use, structural heterogeneity and soil characteristics of the study regions, see Klotzbücher et al. (2015).

We employed a paired study design to detect scale-dependent effects of abiotic conditions and surrounding landscape on the vegetation. In the following, the term “rice field” refers to the entity of a paddy and its bunds, whereas each “site” comprised a rice field irrespective of whether only the vegetation of its bunds or also of its paddy was surveyed during the study. The study sites were selected preferentially according to their accessibility and approachability of farmers during the sampling period. In total, we selected five to eighteen pairs (landscape level) of study sites (plot level) in each region (regional level), resulting in 134 sites, 67 pairs and 7 regions (Table 1.1). Each pair of sites comprised one monoculture site that was entirely surrounded by rice fields, and one structurally more diverse site that shared at least one border with one or more non-paddy habitats (such as agroforests, gardens or grasslands) resulting in “diverse” surroundings (and representing an enhanced habitat diversity). Distance between sites ranged from 40 m to 590 m (mean ± SD: 244 ± 120 m).

4.2.2 Vegetation survey

The vegetation survey was conducted within the framework of an interdisciplinary research project on sustainable rice production (LEGATO; Settele et al. 2018). We established a total of 256 vegetation plots (122 in paddies, 134 on bunds), comprising

16 to 70 plots in each of the seven study regions (Table 1.1). Twelve paddies were abandoned or the crop had changed during the sampling period although the corresponding bunds had already been sampled. Every plot was sampled once between 2012 and 2015, either during wet or during dry season. Vascular plant species were recorded with their cover/abundance values using the nine-class Braun-Blanquet scale (Reichelt & Wilmanns 1973). In each paddy, all vascular plant species were recorded in a representative rectangular plot of 20 m^2. Five 2 m^2 subplots were randomly selected on the bunds, stratified as to sample the vegetation at least once on each side of the paddy, because of their variation in width, shape and stability. Cover-abundance values were transformed into percentages (r = 0.1, + = 0.5, 1 = 2.5, 2m = 2.5, 2a = 10, 2b = 20.5, 3 = 37.5, 4 = 62.5, 5 = 87.5) (Dierschke 1994). The species inventory of the five subplots was pooled and percen tages were averaged to represent plots of 10 m^2 size per bund. Altitude and geographical coordinates were determined by GPS device (Garmin eTrex Vista® HCx) in the center of each study site.

The following works were used for plant identification: Harada et al., 1987, 1993; Soerjani et al., 1987; Pancho and Obien, 1995; Cook, 1996; Ho, 1999, 2000, 2003; Nguyen, 2002; Le, 2007; Nguyen and Nguyen, 2007; eFloras, 2008. Voucher specimens of each plant species were collected and stored in GOET (Herbarium of the University of Göttingen). The taxonomy follows The Plant List (2013).

4.2.3 Environmental variables

Mixed soil samples were collected (10–20 cm depth) from five randomly selected spots per plot and analyzed in laboratories of Göttingen University and the Helmholtz Centre for Environmental Research – UFZ. A conductivity gauge of the type pH538 (WTW GmbH) was used to measure the electrical conductivity (*EC*) in the supernatant suspension of a 1:2.5 soil:H_2O mixture, before assessing the soil pH with a pH meter of the type pH358 (Krannich GmbH & Co.KG). Contents of C_{org} and N_{total} were measured with the Dumas combustion method using a VARIO MAX (elementar), afterwards humus content was estimated (C_{org} × 1,725). Texture was determined on a moist sample of fine earth and through visible characteristics (FAO 2006). Soil moisture was categorized into four levels by visual inspection: 1 - moist but solid soil; 2 - wet and soft soil; 3 - very wet and muddy soil with interspersed puddles; 4 - flooded soil completely covered by water. Fanny Langerwisch from the Potsdam Institute for Climate Impact

Research supplied monthly mean temperatures from the years 2001-2006 based on a time-series dataset (CRU TS 3.0) provided by CRU et al. (2008). The local landscape surrounding each site (variable *LandSur*) was assessed categorically according to the presence (at diverse sites) or absence (at monoculture sites) of non-paddy habitats in their direct proximity. Regional land use intensity and structural diversity classes were taken from Settele et al. (2013).

4.2.4 Data analyses

All statistical analyses were done in R (version 3.5.2; R Core Team 2018). Cultivated species were disregarded. Data of bunds and paddies were treated separately. We used linear mixed-effects models (LME, 'lme4' package version 1.1-19; Bates et al. 2015) with a Gaussian error distribution or generalized linear mixed-effects models (GLMM) with a Poisson error distribution during an explorative model selection process to identify predictor variables with highest explanatory value and significant effect ($p < 0.05$) on our response variables species richness (*S*), Shannon diversity (*H*), and the number of entomophilous plants (insect-pollinated species, i.e. all vascular plants except *Equisetaceae*, *Urticaceae*, graminoids, ferns and submerged hydrophytes; S_{ipo}). Corresponding to the final model residual diagnostics, we decided to use the Poisson GLMM for responses *S* and S_{ipo} in paddies (count data), and Gaussian LME for *S* and S_{ipo} on bunds and *H* in both habitat types. The used predictors were *LandSur*, *MeanTemp*, *pH*, *EC*, *C/N*, *Humus*, *Moisture* (only for paddies) and *Texture* (only for bunds). Correlation among response variables was tested using Kendall's correlation coefficient τ. We did not incorporate altitude in our models due to a correlation with mean annual temperature ($\tau = -0.18$, $p < 0.001$). The variables *Region* and *Landscape* were treated as nested random effects to account for the non-independence of sites within landscapes (or pairs, respectively) and regions. Continuous predictor variables were standardized (mean = 0, SD = 1). All variables are listed in detail in Table 4.1, correlation matrices are given in Appendices A.14 and A.15. Model selection was based on Akaike's Information Criterion (AIC) and residual diagnostics according to Zuur et al. (2010). We used forward selection as former global tests with models including all predictors performed significantly better than their corresponding null models (cf. Blanchet et al. 2008). Predictors that led to the strongest decrease in AIC were included first into our models. We checked for interactions with already included fixed effects before including remaining predictors or their interactions into existing models.

Heteroscedasticity and distribution of residuals were checked visually in diagnostic plots for each model. Collinearity among predictors was detected using variance inflation factors (VIFs, 'car' package version 3.0-6; Fox & Weisberg 2019), with all VIFs < 2 accepted in the final model (Zuur et al. 2010). Fitted Poisson-GLMMs were not overdispersed. We assessed conditional R^2 ('performance' package version 0.4.4; Lüdecke et al. 2020) and marginal R^2 ('r2glmm' package version 0.1.2; Jaeger 2017) for each model before assessing partial R^2 ('r2glmm' package) of corresponding predictors. Explained variances of random terms were calculated manually as the proportion of the total variance of the random effects models. Means of the predictors depending on *LandSur*-levels, habitat types or regions were compared using Two Sample t-Tests if the data was normally distributed, or Wilcoxon-Mann-Whitney tests if non-normally distributed. Pairwise Wilcoxon Rank Sum tests were used for pairwise comparisons of species richness between regions or moisture levels with corrections for multiple testing (Holm).

Table 4.1: List of variables used in GLMMs (generalized linear mixed-effects models) and LMEs (linear mixed-effects models) to identify drivers of plant diversity in Southeast Asian rice ecosystems. Mean annual temperatures were calculated based on a time-series dataset from 2001 to 2006 (CRU TS 3.0). All other variables were measured and recorded on site between 2012 and 2015, or afterwards calculated from sampled values.

	Variable	Description	Unit
Spatial level	*Plot*	Plot-ID; each study site can have two Plot-IDs, i.e. one for the bunds and one for the paddy plot	-
	Landscape	Landscape-ID; each "Landscape" represents one pair of sites (diverse and monoculture)	-
	Region	Region-ID; each "Region" consists of five to thirteen pairs of sites	-
Explanatory variables	*pH*	Soil acidity (10–20 cm below surface)	-
	EC	Electric conductivity (10–20 cm below surface)	µS/cm
	C/N	C_{org}/N_{total} ratio (10–20 cm below surface)	-
	Humus	Humus content = C_{org}*1.725 (10–20 cm below surface)	%
	Texture	Soil textural classes according to the FAO (2006)	-
	Moisture	Soil moisture categorized by four levels of water saturation ("moist", "wet", "very wet", "flooded")	-
	MeanTemp	Mean annual temperature, calculated from monthly mean temperatures of the years 2001 to 2006	°C
	LandSur	Type of surrounding landscape (monoculture vs. diverse) according to the proximity of non-paddy habitats	-
Plant diversity indices	*S*	Species richness (excl. cultivated plants)	-
	H	Shannon diversity (excl. cultivated plants)	-
	S_{ipo}	Number of entomophilous plants (excl. cultivated plants)	-

Analyses of species turnover and composition were performed with the 'vegan' package (version 2.5-4; Oksanen et al. 2019). Singletons and doubletons were eliminated from the dataset before excluding plots without weeds. The terms alpha and beta diversity refer to a wide variety of phenomena with various spatial scales (Tuomisto 2010a). We use these terms as follows: alpha diversity equals the species diversity (*S*, S_{ipo} or *H*) on the plot level, beta diversity quantifies the variation in species composition of plots within a region, between bunds and paddies (across all regions) or between the seven regions. To quantify the compositional dissimilarity between different plots we used the Bray-Curtis coefficient (Bray & Curtis 1957), which ranges between 0 (species composition and abundances between two plots are identical) and 1 (two plots do not share any species). Species turnover within regions (β_{intra}) was calculated with Bray-Curtis dissimilarities between plots based on original species cover-abundances. Regional means were calculated by averaging all β_{intra} values of the corresponding region (mean of all site pairs). Species turnover between regions (β_{inter}) was calculated with Bray-Curtis dissimilarities based on the mean cover-abundance of each species in a region. We also performed detrended correspondence analysis (DCA) on the square root- transformed species data to use the length of axis 1 as a direct measure of species turnover (c.f. Tuomisto 2010b) and to visualize differences in species composition between regions and habitat types.

Kendall's correlation coefficient τ was used to test for correlations of alpha diversity (*S*, S_{ipo} and *H*) between bunds and paddies of the same study site, and between regional means of plot-level species richness and beta diversity (Bray-Curtis dissimilarities between plots) in both habitat types.

4.3 Results

4.3.1 Floristic diversity

A total of 315 plant taxa (117 in paddies, 305 on bunds) were recorded in the studied rice landscapes, belonging to 98 genera and 63 families. We recorded 198 species (or 63% of the total species) exclusively on bunds, ten species (3%) occurred only in paddies and 108 species (34%) in both habitats (Appendix A.5). Ten species were cultivated (mostly intercropped on bunds), 193 species are insect-pollinated and 97 species are red-listed as of "Least Concern" (IUCN 2015). About 40% of all taxa were

recorded less than three times. The mean number of species recorded per plot averaged 27.8 ± 11.7 species on bunds (range: 0–53) and significantly less ($p < 0.001$) in paddies ($S = 6.5 \pm 5.8$, range: 0–29). Species richness was highly correlated with H ($\tau = 0.60$, $p < 0.001$) and S_{ipo} ($\tau = 0.85$, $p < 0.001$) on bunds, and likewise with H ($\tau = 0.80$, $p < 0.001$) and S_{ipo} ($\tau = 0.86$, $p < 0.001$) in paddies. Species richness was also correlated between bunds and paddies of the same study site ($\tau = 0.34$, $p < 0.001$), as were H ($\tau = 0.21$, $p = 0.002$) and S_{ipo} ($\tau = 0.39$, $p < 0.001$).

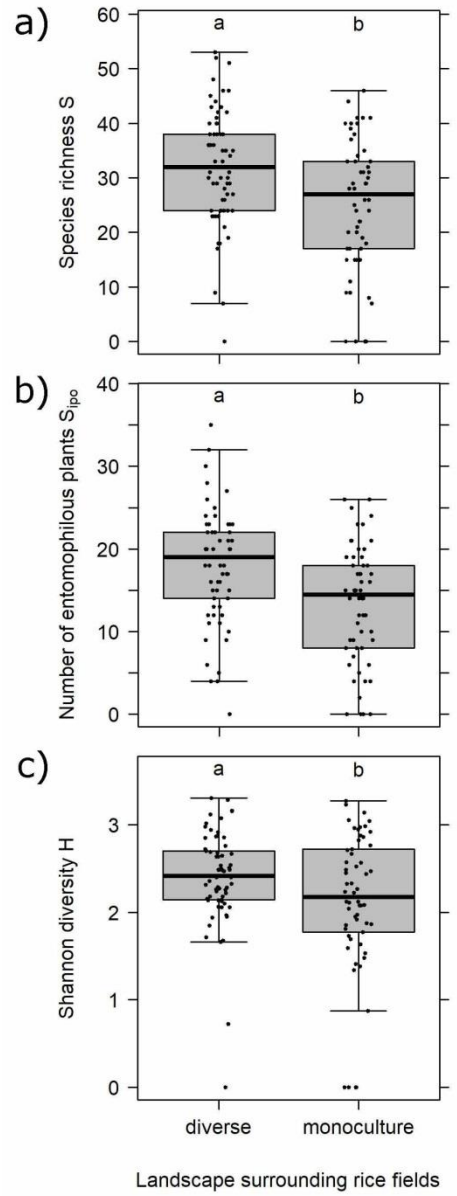

Fig. 4.1: (a) Species richness ($p = 0.001$), (b) numbers of entomophilous plants ($p < 0.001$) and (c) Shannon diversity ($p = 0.046$) of vascular plants on bunds of diverse vs. monoculture sites. Letters indicate significant differences ($p < 0.05$) between levels, n = 123.

4.3.2 Effects of local surroundings and abiotic conditions on the plant diversity of bunds

Surrounding landscape (monoculture vs. diverse; *LandSur*), mean annual temperature and soil pH showed the strongest effects on the plant species richness of bunds (Fig. 4.1a, Table 4.2, Appendices A.16–18). Bunds that were in proximity of non-paddy habitats showed higher species richness (32 ± 10.5, range 0–53) than those that were not (24.9 ± 11.8, range 0–46, p = 0.001). Mean annual temperature had the second most prominent effect and an additional negative effect in interaction with rice monoculture around sites. Below a threshold of about 21 °C, rising temperatures clearly reduced species richness, almost independently of the surrounding landscape, whereas above this point, the decrease in species richness was mitigated in diverse sites (Appendix A.19). Decreasing soil pH generally enhanced species richness on bunds, although this predictor showed the weakest significant effect in our model (Appendix A.20).

Table 4.2: Model estimates of variables with significant effects on plant species richness (*S*), Shannon diversity (*H*) and the number of entomophilous plants (S_{ipo}) on Southeast Asian rice field bunds (n = 123). For full names and details of variables see Table 4.1 (SE = standard error, DF = degrees of freedom).

Response variable	Fixed variable	Estimate	SE	DF	*t*-value	*p*-value	
S	*LandSur*_diverse	30.76	2.66	7.3	11.6	<0.001	***
	*LandSur*_monoculture	-5.73	1.13	69.5	-5.1	<0.001	***
	MeanTemp	-4.69	1.79	28.2	-2.6	0.014	*
	pH	1.87	0.89	99.8	2.1	0.038	*
	*LandSur*_monoculture:*MeanTemp*	-3.17	1.15	78.4	-2.8	0.007	**
S_{ipo}	*LandSur*_diverse	17.37	1.66	7.6	10.4	<0.001	***
	*LandSur*_monoculture	-4.14	0.79	66.9	-5.3	<0.001	***
	MeanTemp	-2.20	1.20	23.4	-1.8	0.079	.
	*LandSur*_monoculture:*MeanTemp*	-2.33	0.80	75.3	-2.9	0.005	**
H	*LandSur*_diverse	2.30	0.16	7.2	14.4	<0.001	***
	*LandSur*_monoculture	-0.23	0.07	66.4	-3.2	0.002	**
	MeanTemp	-0.30	0.12	19.3	-2.5	0.023	*
	*LandSur*_monoculture:*MeanTemp*	-0.25	0.07	72.6	-3.4	0.001	**

Regional differences in species richness were strong, ranging from a mean of 38.7 ± 7.1 species on bunds in VN2 to 7.5 ± 10.5 species on bunds in VN4 (Fig. 4.2a, Table 4.3, Appendix A.17). The patterns found for species richness depending on surrounding landscape, mean annual temperature and soil pH were clearly bound to region-specific effects. For example, regions with cooler mean annual temperatures (i.e. VN3 and PH3)

supported fields with higher and less variable species richness, almost irrespective of the surrounding landscape (Appendix A.19), whereas variation in species richness in relation to soil pH was higher at monoculture sites of these regions, but remained relatively stable between monoculture and diverse sites in all other regions (Appendix A.20).

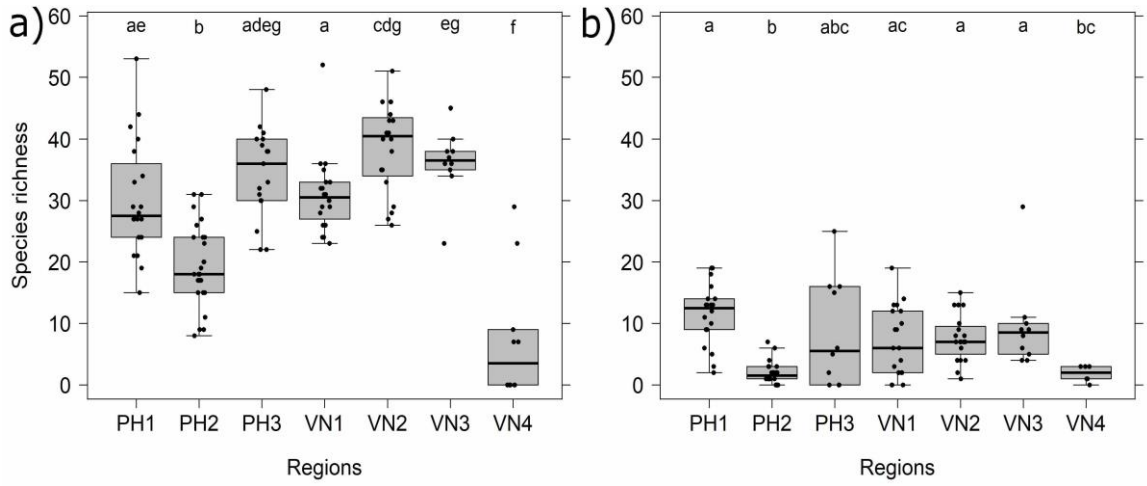

Fig. 4.2: The study regions (for full names see Fig. 1.7) were characterized by distinct levels of plot-level plant diversity (a) on bunds and (b) in paddies. Significant differences ($p < 0.05$) of species richness between regions are indicated with letters, $n_{bunds} = 123$ and $n_{paddies} = 110$.

Models with H and S_{ipo} as response variables showed weaker but mostly similar patterns, although the effects of variable soil pH were not significant (Fig. 4.1b-c, Table 4.2, Appendices A.21 and A.22). Bunds in proximity of non-paddy habitats had in average a higher Shannon diversity (mean: 2.4 ± 0.5) compared to monoculture sites (mean: 2.1 ± 0.8), and also higher richness of entomophilous plants ($mean_{diverse}$: 18.0 ± 6.8 and $mean_{monoculture}$: 13.4 ± 7.0, respectively). Again, H and S_{ipo} were reduced with rising mean annual temperatures, especially at monoculture sites, and varied among the study regions.

Table 4.3: The total number of recorded plots and species, and the regional means (± SD) of species richness (*S*) and of the Bray-Curtis dissimilarities among plots (β_{intra}) for paddies and their bunds. For full names and location of study regions see Fig. 1.7 and Table 1.1.

Study region	Bunds				Paddies			
	N° of plots	Total species	mean *S*	mean β_{intra}	N° of plots	Total species	mean *S*	mean β_{intra}
PH1	20	122	30.1 ± 9.4	0.79 ± 0.12	20	59	11.4 ± 4.9	0.82 ± 0.15
PH2	36	106	18.8 ± 6.6	0.73 ± 0.15	34	27	2.5 ± 2.5	0.83 ± 0.22
PH3	18	121	34.0 ± 7.4	0.69 ± 0.11	12	41	7.2 ± 8.6	0.87 ± 0.19
VN1	20	105	31.0 ± 6.3	0.68 ± 0.12	20	37	6.9 ± 5.7	0.85 ± 0.17
VN2	20	113	38.7 ± 7.1	0.63 ± 0.12	20	43	7.6 ± 3.8	0.90 ± 0.12
VN3	10	98	36.2 ± 5.6	0.62 ± 0.11	10	43	9.5 ± 7.3	0.75 ± 0.19
VN4	10	38	7.5 ± 10.5	0.76 ± 0.25	6	6	1.8 ± 1.3	0.72 ± 0.37

4.3.3 Effects of local surroundings and abiotic conditions on plant diversity in paddies

The only significant effects on the plant diversity in the paddies were related to soil moisture content (Fig. 4.3, Table 4.4, Appendices A.16 and A.17). We observed differences in species richness among all four moisture levels, but not all levels differed significantly from each other ($p < 0.05$). We recognized comparable patterns in the models with *H* or S_{ipo} as response variables, though effects on *H* were weaker (Table 4.4, Appendix A.17).

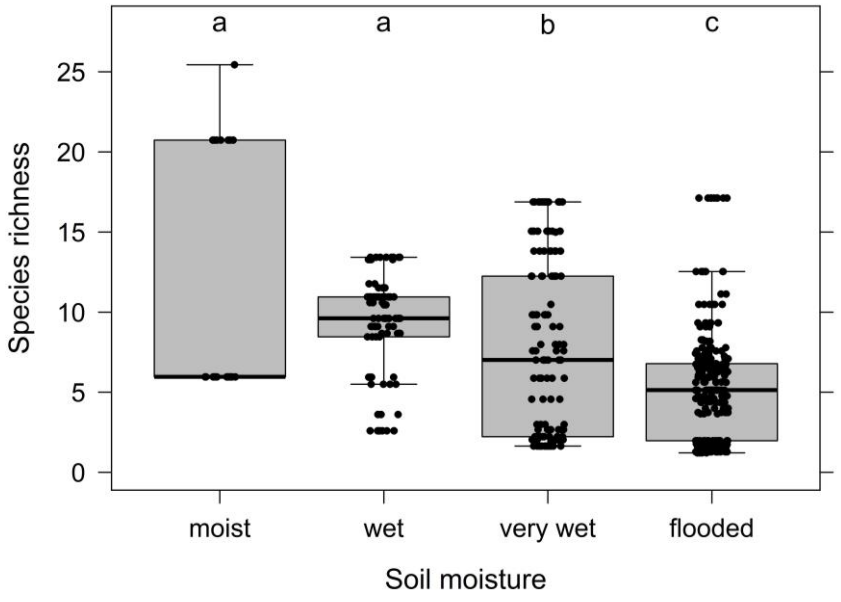

Fig. 4.3: Species richness of vascular plants in paddies depending on soil moisture level. Significant differences ($p < 0.05$) are indicated by letters, n = 110.

Plant species richness ranged from 1.8 ± 1.3 in VN4 paddies to 11.4 ± 4.9 in PH1 paddies, and was more balanced between regions compared to the bunds, though some significant regional differences were found (Table 4.3, Fig. 4.2b). In paddies, regional differences of *H* and S_{ipo} are again comparable to those of species richness (Appendices A.21 and A.22).

Table 4.4: Model estimates of variables with significant effects on plant species richness (*S*), Shannon diversity (*H*) and the number of entomophilous plants (S_{ipo}) in Southeast Asian paddies (n = 110). Estimates of *S* and S_{ipo} are on the log-scale. For full names and details of variables see Table 4.1 (SE = standard error, DF = degrees of freedom).

Response variable	Fixed variable	Estimate	SE	*z*-value	DF	*t*-value	*p*-value	
S	*Moisture*_moist	2.67	0.33	8.1	-	-	<0.001	***
	*Moisture*_wet	-0.75	0.25	-3.0	-	-	0.002	**
	*Moisture*_very wet	-0.93	0.24	-3.8	-	-	<0.001	***
	*Moisture*_flooded	-1.23	0.22	-5.7	-	-	<0.001	***
S_{ipo}	*Moisture*_moist	2.24	0.39	5.7	-	-	<0.001	***
	*Moisture*_wet	-0.80	0.30	-2.7	-	-	0.007	**
	*Moisture*_very wet	-1.25	0.29	-4.3	-	-	<0.001	***
	*Moisture*_flooded	-1.36	0.26	-5.2	-	-	<0.001	***
H	*Moisture*_moist	1.93	0.38	-	45.9	5.1	<0.001	***
	*Moisture*_wet	-0.45	0.36	-	101.1	-1.2	0.218	
	*Moisture*_very wet	-0.86	0.35	-	103.3	-2.4	0.017	*
	*Moisture*_flooded	-0.92	0.33	-	98.9	-2.8	0.006	**

4.3.4 Species turnover

The regional means of the Bray-Curtis dissimilarities among plots (mean β_{intra}) were on average lower between bunds (mean: 0.70 ± 0.06) than between paddies (mean: 0.82 ± 0.07). The highest species turnover was observed between bunds of PH1, and the lowest in VN3. In the paddies, VN2 showed the highest mean β_{intra} and VN4 the lowest (Table 4.3). Mean species richness showed no significant correlation with mean β_{intra}, neither on bunds (τ = -0.61, p = 0.069) nor in paddies (τ = 0.24, p = 0.56).

Bray-Curtis dissimilarities among regions (β_{inter}) were also generally lower on bunds (mean: 0.74 ± 0.09) than in the paddies (mean: 0.85 ± 0.08). Highest dissimilarities were found between upland and lowland regions: on bunds between PH1 and VN3, and in paddies between VN3 and VN4 (Table 4.5). Regions VN1 and VN2 showed the most similar species composition on bunds as well as in paddies.

Table 4.5: Bray-Curtis dissimilarities (β_{inter}) among the study regions (for full names see Fig. 1.7) indicate differences in the species composition in both habitat types. The number of species occurring more than twice is given in parentheses. Lowest values are written in italic letters, highest values in bold letters.

	Bunds (178)						Paddies (102)					
Regions	PH1	PH2	PH3	VN1	VN2	VN3	PH1	PH2	PH3	VN1	VN2	VN3
PH2	0.77	-					0.69	-				
PH3	0.73	0.77	-				0.81	0.93	-			
VN1	0.62	0.77	0.69	-			0.82	0.86	0.81	-		
VN2	0.60	0.81	0.72	*0.47*	-		0.79	0.80	0.93	*0.61*	-	
VN3	**0.87**	0.75	0.81	0.85	0.78	-	0.91	0.93	0.88	0.82	0.88	-
VN4	0.79	0.69	0.83	0.70	0.84	0.75	0.81	0.91	0.91	0.92	0.88	**0.95**

The DCA showed a clear distinction in the species composition of the two habitat types (Appendix A.23): site scores of the bunds are located on the mid to lower left side whereas the paddy scores are spread on the mid to upper right side. Perpendicular to this separation line (from the upper left to the lower right corner of the graph), site scores are aligned in more or less vertical stripes according to their regional affiliation, and thus, highlight the regional differentiation in species composition. An axis length of 5.07 (DCA1) also indicates a complete species turnover along the first axis, and hence between the two habitat types and among the seven regions.

4.4 Discussion

We showed that the local plant diversity can be linked to different abiotic conditions and the presence or absence of non-paddy habitats in proximity of the study sites. Further on, regions and habitat types differ in diversity and composition of rice weeds.

4.4.1 Drivers of rice weed diversity on bunds

The species richness on bunds was mainly influenced by the surrounding landscape, mean annual temperature and soil acidity. The close proximity of other habitat types was the key driver of the plot-level plant diversity (alpha diversity) on rice field bunds probably due to propagule influx from adjacent habitats (mass effect; Shmida & Wilson 1985). Species pools on bunds might profit from the immigration of plants through dispersal from adjacent areas. Such neighborhood effects on plant diversity were described from temperate wheat fields (Gabriel et al. 2005) and subtropical areas dominated by rice and other crops (Zhou et al. 2018). In Indonesia, species richness on bunds with other crops or trees and in multiple-crop landscapes was higher than on

ordinary bunds and in monoculture landscapes (Kumalasari & Bergmeier 2014). In our study regions, species richness is reduced by on average almost 20% in monoculture landscapes, whereas effects on Shannon diversity and the number of entomophilous plants were slightly weaker. In homogenous landscapes, plant diversity levels might also be more prone to indirect negative effects of other variables: monoculture sites showed generally stronger decreases in species richness with rising mean annual temperatures. In mountain sites, soil-acidity dependent species richness variation was higher in monoculture compared to diverse sites. We conclude that plant diversity in structurally complex rice landscapes is more resilient against the effects of agricultural intensification. Neighboring effects might again be enhanced in landscapes of complex composition because of an increased availability of suitable habitats that can serve as refuges and corridors for rice weeds, such as wetlands, grasslands, home gardens, other crop fields or fallows. Besides, plant diversity was influenced by the surrounding landscape in agricultural areas in the tropics (Martínez et al. 2015), the subtropics (Zhou et al. 2018), the Mediterranean (José-María et al. 2010) and temperate regions (Gabriel et al. 2005; Roschewitz et al. 2005; Gaba et al. 2010; Poggio et al. 2013; Maskell et al. 2019).

Regarding climatic conditions, we showed that mean annual temperature had a significant negative effect on plant diversity, especially at higher altitudes and at monoculture sites, perhaps due to higher topographical variation and reduced land use intensity in the uplands. Higher species richness in upland areas was also observed in Indonesian paddies and bunds (Kumalasari 2014), and altitude was identified as an important discriminating factor of plant communities in rice fields of Indonesia (Kumalasari 2014), Nepal (Nowak et al. 2016) and Tajikistan (Nowak et al. 2013). A favorable climate as well as topographic and soil heterogeneity provide suitable conditions for plant life in mountainous regions of North Vietnam and the Philippines. The local farmland flora may also be enriched due to overlapping altitudinal distribution ranges of temperate/subtropical and tropical plant species in mid-elevations, as reported in studies on the diversity of introduced plants from other tropical mountain areas (Tassin & Rivière 2003; Jakobs et al. 2010). Fried et al. (2017, 2018) found several genera in the species pools of PH3 and VN3 that are common to temperate regions. At some sites, the negative effects of high temperatures may be weakened by advantageous macro- and microclimatic conditions. However, the question why plant diversity

independent of regional affiliation decreased with higher temperatures remained yet unresolved. This effect may well result from higher land use intensity in the hot lowlands, but biogeographical reasons may also exist (higher species pools outside lowlands). We tried to create meaningful land use indices and incorporate them (as well as information about local weed management strategies) into our models, but weed management was too heterogeneous among study regions to allow for a proper statistical analysis of our data. However, land use intensity in a particular region (e.g. in the mountain region Lao Cai, VN3) was not generally lower in fields at high altitudes (with cooler temperatures) than in fields at low altitudes (with higher temperatures) in the same region, whereas in regional comparison, highland regions generally use less input of synthetic fertilizers and pesticides than lowland regions. Most probably, land use intensity is the best explanation for differences of plant diversity between regions (see Fig. 4.2), but not within each region. In our analyses, we included "Region" (and with it also region-specific differences, e.g. the strong differences of land use intensity) in the random term of our models to reveal region-independent variables with effects within regions. Mean annual temperature, in contrast to any land use index or weed control method, thus had a region-independent effect on plant diversity. We also used partial datasets (e.g. by excluding VN4 or by restriction to only lowland/highland regions) during model selection to ensure that we do not have statistical artefacts due to the distinctiveness of the study regions (e.g. because of their distinct weed management or climate) but the variables with significant effects remained the same among the models of the partial datasets. Future studies might focus on a particular region (with more local data) or provide more intersecting data to enable a sound statistical solution of the effect of land use intensity (or weed management) on plant diversity.

Plant growth and development depends on the availability of soil nutrients which leads to competition between rice plants and weeds, and thus influences species distributions. The availability of nutrients to plants is bound to the soil acidity making it an important chemical property of rice soils (Fageria et al. 2011). Soil pH can influence the germination and composition of rice weeds (Singh & Singh 2009). Our previous studies in the study area have already identified soil acidity as a major determinant of the arable species composition (Fried et al. 2017, 2018). Our new findings also indicate a significant, region-independent increase of vascular plant diversity with decreasing soil

acidity. Soil measurements are desirable in further rice vegetation analyses to explain interactions between soil, management, crop and weeds in more detail.

4.4.2 Drivers of rice weed diversity in paddies

Species diversity in paddies was much lower than on bunds, which corresponds to findings from China (Nemoto & Otsuka 2014), Indonesia (Kumalasari 2014), Japan (Fukamachi et al. 2005), and Sri Lanka (Bambaradeniya et al. 1998). Impacts of agricultural management, i.e. flooding, weed control and seeding, are generally more severe in paddies and lead to a comparatively depauperate and uniform flora. Particularly soil moisture was significantly negatively correlated with plant diversity in paddies. These findings are consistent with other studies on effects of water depth and availability on weed diversity and/or composition in tropical and subtropical paddies (Bambaradeniya et al. 1998; Tomita et al. 2003; Juraimi et al. 2011; Kumalasari 2014; Nowak et al. 2015, 2016). Proper water management has been the traditional method of weed control long before synthetic herbicides became available. Standing water suppresses weed growth directly by reducing plant germination and establishment, and indirectly through the inherent size advantage of the crop (Tuong et al. 2005). Different strategies concerning level, duration and timing of flooding have been proposed, though most agree that flooding in the early stages of crop establishment reduces weed growth most effectively (e.g. De Datta 1981; Williams et al. 1990; Bhagat et al. 1996; Hill & Mortimer 2001; Chauhan 2013), but distribution, growth and reproduction vary between species and soil moisture levels (e.g. Arai et al. 1955; De Datta 1981; Bhagat et al. 1996; Morita & Kabaki 2002; Kamoshita et al. 2010; Juraimi et al. 2011). C3 plants might outcompete C4 plants under water-saturated conditions (Tanaka 1976), and flooding speed and intermittent draining might affect particularly algae and aquatic weeds (Hill et al. 1994). Sound knowledge on local species composition and community variation is essential to detect specific plant functional groups with beneficial effects for the local rice ecosystems and may help in adapting management strategies to make rice production more sustainable. Seasonal changes in rainfall and humidity should be less important in irrigated landscapes of permanent water availability, especially with respect to paddy vegetation. Temperature seasonality is pronounced particularly in the mountains (VN3 and PH3) where rice cultivation, and accordingly the sampling of the vegetation, was restricted to the wet season. Only some rice fields in the lowland

regions were sampled in the dry season where temperature seasonality effects should be negligible.

The proximity of non-paddy habitats showed no significant effect on species richness. This corresponds to findings from Indonesia, where nearby semi-natural vegetation did not enhance species richness in paddy fields, but on bunds (Kumalasari & Bergmeier 2014). In Mediterranean cereal fields, landscape heterogeneity influenced plant diversity on boundaries and field edges, but not in field centers (José-María et al. 2010). Paddies are highly disturbed and unsuitable habitats for other plants than rice and its most closely associated weeds, so weed control effects might displace those related to the surrounding landscape. Additionally, rice plant communities are often fragmentary and characterized by comparatively low species richness (Miyawaki 1960), making drivers of paddy plant diversity even harder to detect. This could as well be a reason why regional differences in plot level (alpha) diversity in paddies were weaker than on bunds. Nevertheless, effects of environmental conditions on the composition of the local plant communities of paddies were recently revealed (Fried et al. 2017).

4.4.3 Region-specific effects on the weed diversity

Apart from drivers of plant diversity acting in all regions, we found regional differences of alpha diversity that can only be explained by region-specific factors. We documented severely decreased plant diversity at the study sites in the Mekong Delta (VN4), and to a lesser degree in Nueva Ecija (PH2), probably resulting from the highly intensive agricultural production methods and the consequently rather monotonous local landscape. In contrast, relatively high levels of plant diversity were observed in the heterogeneous rice terrace landscapes of Ifugao (PH3) and Lao Cai (VN3), where the usage of fertilizers, herbicides and machinery is reduced and the climate allows for only one rice crop per year. Rice agroecosystems in mountains are often characterized by traditional upland rice cultivars, reduced application of synthetic fertilizers and herbicides, and by selective manual weed control (De Datta 1981; Roder 1997; Roder et al. 1997; Galinato et al. 1999; Husson et al. 2001; Doanh & Tuan 2004; Paudel 2011; GRiSP 2013). Regional rice weed diversity surely profits from specific traditional cultivation methods and high local landscape heterogeneity. Recently, Fried et al. (2017, 2018) documented the distinct weed control and cultivation methods of each study

region. Land use practices and intensity vary so greatly among regions that no region-independent variable with general effects on the plant diversity was detected.

4.4.4 Species turnover across sampling plots, between the paddies and their bunds, and between regions (beta diversity)

On bunds, Bray-Curtis dissimilarities between the plots revealed moderate species turnover within regions. There was a tendency of beta diversity to decrease with increasing alpha diversity, land use intensity and declining regional landscape heterogeneity, but we did not detect any significant correlation. Interestingly, species turnover across bunds of the rice terraces in the mountain regions Ifugao and Lao Cai was rather low despite high species numbers (in relation to the number of recorded plots) and alpha diversity, low land use intensity, and overall high regional landscape heterogeneity. In the hilly lowland of Vinh Phuc the pattern was similar. A reason for this might be a higher chance of recording shared species when the number of species per site increases. In contrast, species turnover was high across bunds in PH2 and VN4, where alpha diversity is low due to very intensive monoculture rice production, up to three crop cycles per year, and frequent application of herbicides (also on bunds) (Fried et al. 2018). Low species richness as in regions VN4 and PH2 with even the more common plant species occurring only sparsely cause high species turnover rates on bunds. Such effects might be compensated by larger sampling effort. The highest beta diversity on bunds was documented from Laguna on Luzon Island, where we had moderate species richness but an ample list of species that occurred sparsely and irregularly (cf. Fried et al. 2018). In paddies, lowest species turnover rates were found in the two contrasting regions VN3 and VN4, but no general pattern of beta diversity and its drivers could be revealed. Similar studies are not known to us, so we recommend future research in this field.

We also found high levels of species turnover between regions. The Bray-Curtis dissimilarities shown in Table 4.3 underlined the strong differences in the species composition between regions that we presented in the DCA results. These findings are reflected by previous overall floristic inventories of rice fields in Vietnam and the Philippines (Moody 1989). Geographical variability in climate and soil (least in close regions like VN1 and VN2), and differences in agricultural management (especially between uplands and lowlands) are the main factors characterizing the local rice weed

communities (Fried et al. 2017, 2018). Regional differentiation might further be driven by historical events like isolation, migration and speciation.

Our results of DCA and Bray-Curtis dissimilarities might be influenced by excluding rare species (40% of the recorded taxa) although this is a common practice to avoid noise in multivariate analyses (c.f. Poos & Jackson 2012). Nonetheless, we found many more species on bunds than in paddies, while previous studies have already shown that almost half of the recorded taxa in paddies occurred in less than 2% of the plots (Fried et al. 2017). We assume that a high rate of propagule influx from bunds (and perhaps irrigation channels) may enrich the local paddies' species inventory with casual plants, depending entirely on the reproductive success in adjacent habitats. The correlations of plot-level plant diversity (*S*, S_{ipo} and *H*) between bunds and paddies of the same study site support this assumption. Similar neighborhood effects are known from subtropical rice production sites in South China (Zhou et al. 2018) as well as from temperate wheat fields (Gabriel et al. 2005). The predominant life form in paddies, annual amphibious plants (Bolòs & Masclans 1955; Miyawaki 1960; Fried et al. 2017), is particularly capable of supporting sink populations in hostile environments through high seed production, dispersal and regeneration rates (cf. Kunin 1998; Santamaría 2002). Bunds host the majority of rice weeds, in numbers and cover, and serve as an important source, refuge and corridor of plants in rice agroecosystems (Fried et al. 2018). They are an important and integral part of the rice agroecosystem with a distinct flora and vegetation and play a key role in the Southeast Asian agrobiodiversity.

4.5 Conclusion

We found great regional variability in the plant species composition of local rice production landscapes. Neighboring habitats play an important role as source habitats for propagules of plant species in rice fields. Especially bunds represent important habitats for plant species that are not necessarily harmful to rice cultivation. Bunds and direct neighborhoods of rice fields could contribute to sustain and promote biodiversity of plants and associated animals, such as pollinators and parasitoids of pests or other pest antagonists, in rice production landscapes. In the study area, closer proximity to structurally more complex habitats led to higher numbers of entomophilous plants on bunds, while pollinator diversity, their functional diversity and plant-pollinator network complexity increased in rice fields and home gardens (Hass et al. 2018; Schrader et al.

2018) compared to those in monoculture. Diversification of rice agroecosystems through the protection and promotion of plant biodiversity may also lead to higher resilience against disturbances, but species composition and preservation of native species should have greater priority than conservation of species richness per se (Tylianakis et al. 2010). High plant species diversity can be conserved or promoted by reduced management intensity, conservation and restoration of extensively managed habitats, such as agroforests, and irrigation schemes that help to reduce pesticide inputs. Sustainable rice production systems should take care of biodiversity and the proper management of the bunds. Targeted managements of plant species on the bunds could prove as a potential measure for ecological engineering (Settele et al. 2018) and promote multiple ecosystem services, including pest control and pollination (Westphal et al. 2015), in rice landscapes that often comprise a mosaic of home gardens, orchards and rice paddies.

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Chapter 5:

Synthesis

5.1 Key findings

5.1.1 Diversity and composition of local rice weed species and life forms in paddies and on bunds

During the course of this thesis, several similarities in the diversity and composition of rice weeds and life forms between the local bunds and paddies were revealed. With regard to the floristic inventory, mostly graminoids of the families *Poaceae* and *Cyperaceae* were found in both habitat types, but also dicot herbs of the families *Asteraceae*, *Linderniaceae*, *Lythraceae* and *Onagraceae* occurred regularly. The species most commonly recorded were *Fimbristylis littoralis*, *Alternanthera sessilis*, *Ludwigia hyssopifolia* and *Lindernia antipoda*, all widely distributed and at least occasionally noxious rice weeds in tropical and subtropical Asia (Soerjani et al. 1987; Kraehmer et al. 2016). In total, about one third of all recorded species were found on both bunds and paddies, and both habitat types show a close floristic relationship with the amphibious vegetation of natural wetlands. Besides these floristic similarities, bunds and paddies in the surveyed study regions were both characterized by strong regional differences of floristic composition and diversity, resulting mainly from geographical variability in climate and soil and the differences in agricultural management. In both habitat types, the highest compositional dissimilarities were found between highland and lowland regions, and the lowest rice weed diversity was recorded in the lowland regions with most intensive rice production and vast monoculture areas. In terms of life form composition, mostly annual, amphibious life forms occurred in the two habitat types as they are best adapted to the cultivation practices and often rapidly changing environmental conditions of rice agroecosystems. This corresponds to findings from previous research on the rice weed flora of southern Europe (Bolòs & Masclans 1955) and Japan (Miyawaki 1960). Further, we found that several taxa in bunds and paddies are uncommon or rare in the study area, and that most of the wild species growing in bunds (57% of all recorded species) and paddies (65%) are known to be used for at least one purpose (e.g. food, medicine, fodder etc.) (eFloras 2008; IUCN 2015).

Apart from the above-mentioned similarities, also several distinct features of the two habitat types were documented. Perhaps the most obvious difference is that species richness and cover were much higher on bunds than in paddies, which is consistent with findings from Indonesia (Kumalasari 2014), Sri Lanka (Bambaradeniya et al. 1998),

China (Nemoto & Otsuka 2014), and Japan (Fukamachi et al. 2005). This fact is further emphasized as about two thirds of all taxa recorded during this vegetation survey were found exclusively on bunds. In contrast, the paddy vegetation is generally rather fragmentary and species-poor (Miyawaki 1960), although the documented species richness in Vietnamese and Philippine paddy weed communities is comparable to that of rice phytocoenoses in Central and Southeast Asia (Nowak et al. 2013, 2015, 2016; Kumalasari 2014). Nevertheless, species numbers and cover were low and only a small minority of all recorded taxa occurred exclusively in paddies. Further, we found that soil moisture was the main determinant of the variation of local paddy weed diversity corresponding to findings in other studies on effects of water regime on weed composition and/or diversity in subtropical and tropical paddies (Bambaradeniya et al. 1998; Tomita et al. 2003; Juraimi et al. 2011; Kumalasari 2014; Nowak et al. 2015, 2016). Few plants are able to persist in paddies for longer periods due to water management and other weed control measures, whereas bunds host the majority of rice weeds, in numbers and cover. Many plant species that are not necessarily noxious rice weeds can use bunds, besides other adjacent habitats like orchards and homegardens, as source, refuge and corridor habitats. The small species inventory of paddies may be supported by propagule influx from the comparably species-rich bunds and neighborhood habitats (mass effect; Shmida & Wilson 1985). Such neighborhood effects are known from subtropical areas dominated by rice and other crops (Zhou et al. 2018) but also from temperate wheat fields (Gabriel et al. 2005). Similar mechanisms might as well influence the vegetation on bunds as we found that surrounding landscape, i.e. the proximity of non-rice habitats, was the key driver of the bunds' weed diversity. A comparable study in Java revealed that species richness on ordinary bunds and in monoculture landscapes was lower than on bunds with other crops or trees and in multiple-crop landscapes (Kumalasari & Bergmeier 2014). Other major factors influencing weed diversity on Vietnamese and Philippine bunds were temperature and soil acidity. Besides, our findings have shown that regional differences in plot-level weed diversity (alpha diversity) were stronger on bunds than in paddies, whereas species turnover (beta diversity) was generally lower on bunds, within and among regions. With respect to the life form composition, many hydrophytes, particularly free-floating plants, occurred in the aquatic to semi-aquatic paddies, but were mostly absent on the terrestrial bunds.

5.1.2 Community composition and environmental conditions

In chapters 2 and 3, the main vascular plant communities of paddies and their bunds in major rice-producing regions of Vietnam and the Philippines were presented. The detailed descriptions were complemented by multivariate analyses of floristic composition and diversity, height and cover of crop and associated weeds, soil properties, climate, altitude, landscape heterogeneity, geographic location, seasonality, and management and intensity of cultivation to identify the main environmental drivers and phytogeographic patterns that shape the local rice weed communities. The variation in species composition with respect to habitat type and regional distribution was highlighted in chapter 4. Our findings confirmed that bunds and paddies are characterized by distinct weed communities (Barrett & Seaman 1980), and that the floristic composition and distribution of rice weeds serve as key indicators of field conditions (Moody & Drost 1983).

In chapter 2, we divided the paddy vegetation in the study area into four main rice weed communities that had not been described before: the ***Fimbristylis littoralis-Leptochloa chinensis*** **community**, the ***Paspalum distichum-Hydrolea zeylanica*** **community**, the ***Echinochloa crus-galli*** **community**, and the ***Rotala indica-Monochoria vaginalis*** **community**. All four communities belong to the phytosociological class of Eurasian rice field vegetation *Oryzetea sativae* Miyawaki 1960 and may be classified into the alliance *Ludwigion hyssopifolio-octovalvidis* Nowak et al. 2015 (in the order *Cypero difformis-Echinochloetalia oryzoidis* O. de Bolòs et Masclans 1955) as they show floristic similarities to other tropical rice weed communities in Indonesia (Kumalasari 2014), Thailand (Nowak et al. 2015) and Nepal (Nowak et al. 2016). Moreover, the floristic inventory of paddy communities is related to syntaxa of semi-natural wetlands and of agrarian landscapes, like in other paddies around the world (Bolòs & Masclans 1955; Miyawaki 1960; Piccoli & Gerdol 1981; Kim 2001). Two of the newly described weed communities (the *Fimbristylis littoralis-Leptochloa chinensis* community and the *Rotala indica-Monochoria vaginalis* community) were further divided into regional subunits. Major discriminating factors for the differentiation of weed communities in Vietnamese and Philippine paddies were soil conditions, temperature and elevation, crop stage, and geographic distribution. Besides, the weed communities were characterized by distinct levels of species richness reflecting cultivation intensity and status of the rice fields.

In chapter 3, we focused on the bunds and classified six main weed communities: the ***Cynodon dactylon-Cyperus rotundus*** **community**, the ***Leptochloa chinensis-Leersia hexandra*** **community**, the ***Kyllingia nemoralis-Ischaemum polystachyum*** **community**, the ***Paspalum distichum-Hydrocotyle sibthorpioides*** **community**, the ***Cuphea carthagenensis-Fimbristylis aestivalis*** **community**, and the ***Rotala indica-Cyperus haspan*** **community**. The latter two are characteristic for bunds in mountain regions, whereas the remaining four occurred exclusively in lowland regions. The newly described bund communities show strong floristic relations to the *Oryzetea sativae*, but they comprise also species of various other phytosociological classes. Particularly strong linkages to communities of trampled grassy habitats (*Eragrostietalia, Plantaginetalia asiaticae* Miyawaki 1964) and dry segetal communities (*Stellariatea mediae*) were revealed (c.f Mucina et al. 1991, 2016). Hence, we conclude that the therophyte-rich ruderal wetland vegetation on bunds constitutes a mosaic-like complex of wet and dry segetal communities interspersed with fragments of communities of trampled habitats. Besides compositional dissimilarities and distinct levels of species richness, the bund communities were mainly differentiated according to geographic position, elevation and temperature, seasonality, soil conditions, and cultivation methods and intensity. Generally, the bund communities showed a much stronger geographic differentiation than the paddy communities.

5.1.3 Weed control and cultivation methods

The floristic composition and diversity of bunds and paddies depends on the choice of cultivation method and weed management strategy (Rao et al. 2007). Weed control methods vary between bunds and paddies according to their different constitution and function. In the paddies, weeds are generally unwanted because they compete with the crop for nutrients, light, space and water (De Datta 1981; Webster 2014). In contrast, bunds are rather seldom planted with crops, particularly in the local lowland regions, but serve mainly as water boundaries and pathways. Nevertheless, bunds were subject to weed control because competitive rice weeds can use bunds as refuge and corridor to invade paddies. Additionally, rice weeds have often been perceived as host plants of rice pests and diseases in the past (De Datta 1981), and farmers might still fear a loss of reputation if the weed vegetation grows too "wild". The most common weed control measures on surveyed bunds were manual weeding by cutting and pulling, and herbicide application. All surveyed paddies were flooded for at least part of the crop

cycle which is probably the most effective method of weed control in rice fields (Rao et al. 2007). Other common weed control measures were puddling and harrowing during land preparation, herbicide application, and manual weeding. Besides, rice plants were almost always transplanted onto the paddies in the study regions. Bunds and paddies have in common that differences in weed management and cultivation methods were most pronounced between highland and lowland regions, which corresponds to observations in Java (Kumalasari 2014). Several characteristic features of highland rice agroecosystems, e.g. intensive manual labor, reduced application of machinery and agrochemicals (fertilizers and pesticides), and only one rice harvest per year, distinguish the rather traditional rice cultivation on terraced paddies from the more intensive rice production in the lowland regions, where at least two crop cycles per year are possible, monoculture areas are more widespread, and more machinery and agrochemicals are applied.

5.2 Concluding remarks and future perspectives

Vietnam and the Philippines are considered as biodiversity hotspots with high plant species richness and endemism, but this diversity is threatened by high rates of habitat loss through deforestation and rapid growth of agricultural production (Myers et al. 2000; Sodhi et al. 2010). The two countries have huge areas under rice cultivation as they are both among the top ten rice producing countries of the world (FAO 2020). The biodiversity in local rice landscapes must be preserved because biodiversity sustains vital ecosystem services (e.g. biocontrol, pollination), enhances the resilience of ecosystems against external pressures (e.g. management mistakes, adverse effects of climate and land use change), and besides, cannot be sufficiently conserved in protection areas alone (Fischer et al. 2006). Recently, efforts to conserve the biodiversity and enhance the sustainability of rice agroecosystems have increased, e.g. in southern Europe (Rossi et al. 2015), Brazil (Maltchik et al. 2011, 2017), China (Luo et al. 2014) and Japan (Yamada et al. 2007). In the framework of an interdisciplinary project focused on a long-term sustainable development of irrigated rice landscapes (LEGATO; Settele et al. 2018), this thesis aimed at a more comprehensive understanding of the floristic diversity and composition of rice weed communities in Vietnam and the Philippines. Our findings provide new insights into the composition and functioning of irrigated rice environments. The considerable variation in climate,

landscape heterogeneity, edaphic conditions, agricultural management and biodiversity of local rice landscapes supports great temporal and spatial variability in the composition of plant species and communities. In turn, community composition effectively indicates management intensity and informs on environmental and biogeographical conditions. Nevertheless, some mechanisms remain unclear and various variables, such as land use intensity, weed management, climate, soil conditions, and species turnover, need to be incorporated into future rice vegetation analyses to disentangle their effects on crop and weeds in more detail. I further recommend repeated sampling (minimum two times) in paddies during the crop cycle as we found community variation along the different crop stages. In this study, the paddy vegetation was sampled only once during a cropping season, either during wet or during dry season, because of the large number of study regions, enormous local bureaucratic efforts, and the lack of trained locals who could survey the vegetation on their own. Future studies should focus on less study regions, or provide more trained personnel to allow for simultaneous sampling in different locations, crop stages and seasons. Besides, future research on plant assemblages of ditches and rice terrace walls is advisable to complement our knowledge on the composition and functioning of entire rice agroecosystems.

The floristic inventory of the local bunds and paddies suggests that a large number of specialized plant species is associated with rice cultivation in Vietnam and the Philippines. To my knowledge, information on the local and regional distribution of most recorded species and their potential value for rice agroecosystems is scarce, but many of them seem to be declining globally (IUCN 2015) and future efforts to conserve their populations and habitats should be considered. Particularly the bunds are an essential and fundamental component of irrigated rice landscapes and play a key role in the Southeast Asian agrobiodiversity because they host a number of useful and rare plants, support a mosaic of specialized weed communities, and provide several beneficial services to the valuable rice agroecosystem. Further, propagule influx from adjacent habitats of rice fields like orchards and homegardens can support weed populations in bunds and paddies with plants that are not necessarily harmful (or might even be beneficial) for rice production. Decreasing biodiversity is a major problem of rice production in the study area (Nguyen et al. 2018) and hence, bunds and neighborhood habitats could contribute to sustain and promote biodiversity of plants

and associated animals, such as pollinators and pest antagonists, in local rice landscapes. High biodiversity can be conserved or promoted by reduced management intensity (including less use of agrochemicals and adapted irrigation schemes), and conservation and restoration of extensively managed habitats in the proximity of rice fields. At the same time, the establishment of more sustainable cropping systems might lead to improvements in food production in rice landscapes while simultaneously sparing land and conserving biodiversity. For example, crops were found at some study sites, such as taro (*Colocasia esculenta*) and water spinach (*Ipomoea aquatica*), that can be grown on bunds, in ditches and ponds, or in rotation or intercropping systems with rice in paddies. Recent studies suggest that intercropping with water spinach is a feasible option for sustainable rice cultivation as it improves yields, pest and disease control, and land use efficiency (Liang et al. 2016; Ning et al. 2017). Further, the selective management of plant species on bunds as a measure of ecological engineering might promote biodiversity and multiple ecosystem services, including pest control and pollination (Westphal et al. 2015; Settele et al. 2018). The knowledge on the local species composition and community variation presented in this thesis can serve as a valuable contribution to the identification of plants with beneficial effects for local agroecosystems, to biodiversity conservation, and to the development of management strategies to make food production in rice landscapes more sustainable.

References

Alexandratos, N. & Bruinsma, J. 2012. World agriculture towards 2030/2050: the 2012 revision. FAO, Rome, IT.

Ali, M.P., Bari, M.N., Haque, S.S., Kabir, M.M.M., Afrin, S., Nowrin, F., Islam, M.S. & Landis, D.A. 2019. Establishing next-generation pest control services in rice fields: eco-agriculture. Scientific reports 9(1): 10180.

Altieri, M.A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment 74(1–3): 19–31.

Arai, M., Miyahara, M. & Yokomori, H. 1955. [Ecological studies on weeds on arable land. IV. On the types produced by adaptation to the soil water of weeds.]. J. Kanto-Tokai Agr. Exp. Stn. 8: 56–62.

Armengot, L., José-María, L., Blanco-Moreno, J.M., Romero-Puente, A. & Sans, F.X. 2011. Landscape and land-use effects on weed flora in Mediterranean cereal fields. Agriculture, Ecosystems & Environment 142(3-4): 311–317.

Bambaradeniya, C.N.B. & Amerasinghe, F.P. 2003. Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63. International Water Management Institute, Colombo, LK.

Bambaradeniya, C.N.B., Fonseka, K.T. & Ambagahawatte, C.L. 1998. A preliminary study of fauna and flora of a rice field in Kandy, Sri Lanka. Ceylon Journal of Science 25: 1–22.

Barrett, S.C.H. & Seaman, D.E. 1980. The weed flora of Californian rice fields. Aquatic Botany 9(0): 351–376.

Barthlott, W., Mutke, J., Rafiqpoor, D., Kier, G. & Kreft, H. 2005. Global centers of vascular plant diversity. Nova Acta Leopoldina 92(342): 61–83.

Bassa, M., Boutin, C., Chamorro, L. & Sans, F.X. 2011. Effects of farming management and landscape heterogeneity on plant species composition of Mediterranean field boundaries. Agriculture, Ecosystems & Environment 141(3-4): 455–460.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48.

Bhagat, R.M., Bhuiyan, S.I. & Moody, K. 1996. Water, tillage and weed interactions in lowland tropical rice. A review. Agricultural Water Management 31(3): 165–184.

Biodiversity Center of Japan, Ministry of Environment 2013. Red list of threatened plants of Japan. URL: http://www.biodic.go.jp/english/rdb/rdb_f.html. Accessed 21 July 2016.

Blanchet, F.G., Legendre, P. & Borcard, D. 2008. Forward selection of explanatory variables. Ecology 89(9): 2623–2632.

Blume, H.-P., Brümmer, G.W., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K. & Wilke, B.-M. 2016. Scheffer/Schachtschabel Soil Science. 1st ed. Springer, Berlin, DE.

Bolòs, O. de & Masclans, F. 1955. La vegetacion de los arrozales en la region mediterranea. Collectanea Botanica IV(32): 415–434.

Bouman, B., Barker, R., Humphreys, E., To Phuc Tuong, Atlin, G., Bennett, J., Dawe, D., Dittert, K., Dobermann, A., Facon, T., Fujimoto, N., Gupta, R.K., Haefele, S.M., Hosen, Y., Ismail, A.M., Johnson, D., Johnson, S., Khan, S., Lin Shan, Masih, I., Matsuno, Y., Pandey, S., Peng, S., Thiyagarajan, T.M. & Wassmann, R. 2007a. Rice: Feeding the billions. In: Molden, D. (ed.) Water for food, water for life: a comprehensive assessment of water management in agriculture, pp. 515–549. International Water Management Institute, Colombo, LK.

Bouman, B., Humphreys, E., Tuong, T.P. & Barker, R. 2007b. Rice and Water. In: Sparks, D.L. (ed.) Advances in Agronomy, pp. 187–237. Elsevier Academic Press Inc., San Diego, US.

Bray, J.R. & Curtis, J.T. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecological Monographs 27(4): 325–349.

Burkhard, B., Müller, A., Müller, F., Grescho, V., Anh, Q., Arida, G., Bustamante, J.V., van Chien, H., Heong, K.L., Escalada, M., Marquez, L., Thanh Truong, D., Villareal, S. & Settele, J. 2015. Land cover-based ecosystem service assessment of irrigated rice

cropping systems in southeast Asia – An explorative study. Ecosystem Services 14: 76–87.

Burnham, K.P. & Overton, W.S. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60(5): 927–936.

Carni, A. & Mucina, L. 1998. Vegetation of trampled soil dominated by C4 plants in Europe. Journal of Vegetation Science 9(1): 45–56.

Carretero, J.L. 1988. Rice field flora and vegetation in the provinces of Valencia and Tarragona. Collectanea Botanica 17(1): 113–124.

Carretero, J.L. 1989. La vegetación emergente de los arrozales europeos. Anales de Biología 15(4): 135–141.

Castonguay, A.C., Burkhard, B., Müller, F., Horgan, F.G. & Settele, J. 2016. Resilience and adaptability of rice terrace social-ecological systems. A case study of a local community's perception in Banaue, Philippines. Ecology and Society 21(2).

Chauhan, B.S. 2013. Management strategies for weedy rice in Asia. International Rice Research Institute, Los Baños, PH.

Cohen, J.E., Schoenly, K., Heong, K.L., Justo, H., Arida, G., Barrion, A.T. & Litsinger, J.A. 1994. A Food Web Approach to Evaluating the Effect of Insecticide Spraying on Insect Pest Population Dynamics in a Philippine Irrigated Rice Ecosystem. Journal of Applied Ecology 31(4): 747–763.

Cook, C.D.K. 1996. Aquatic and wetland plants of India. Oxford University Press, New York, US.

Coronas, J. 1920. The climate and weather of the Philippines, 1903 to 1918. Bureau of Printing, Manila, PH.

CRU – University of East Anglia Climatic Research Unit, Jones, P.D. & Harris, I. 2008. Climatic Research Unit (CRU) time-series datasets of variations in climate with variations in other phenomena. URL: http://catalogue.ceda.ac.uk/uuid/3f8944800cc48e1cbc29a5ee12d8542d. Accessed 15 July 2015.

Cunningham, S.A., Attwood, S.J., Bawa, K.S., Benton, T.G., Broadhurst, L.M., Didham, R.K., McIntyre, S., Perfecto, I., Samways, M.J., Tscharntke, T., Vandermeer, J., Villard, M.-A., Young, A.G. & Lindenmayer, D.B. 2013. To close the yield-gap while saving biodiversity will require multiple locally relevant strategies. Agriculture, Ecosystems & Environment 173: 20–27.

Dawe, D. 2013. Geographic determinants of rice self-sufficiency in Southeast Asia. FAO, Rome, IT.

De Datta, S.K. 1981. Principles and practices of rice production. John Wiley & Sons, Singapore, SG.

De Datta, S.K. & Feuer, R. 1975. Soils on which upland rice is grown. In: IRRI (ed.) Major Research in Upland Rice, pp. 27–39, International Water Management Institute, Los Baños, PH.

Deil, U. 2005. A review on habitats, plant traits and vegetation of ephemeral wetlands: a global perspective. Phytocoenologia 35(2-3): 533–706.

Dierschke, H. 1994. Pflanzensoziologie. Grundlagen und Methoden. Ulmer, Stuttgart, DE.

Doanh, Q. & Tuan, H.D. 2004. Improving indigenous technologies for sustainable land use in northern mountainous areas of Vietnam. Journal of Mountain Science 1(3): 270–275.

Edirisinghe, J.P. & Bambaradeniya, C.N.B. 2006. Rice fields: an ecosystem rich in biodiversity. Journal of the National Science Foundation of Sri Lanka 34(2): 57.

eFloras 2008. Flora of China. URL: http://www.efloras.org. Accessed 22 Sept 2015.

Egli, L., Meyer, C., Scherber, C., Kreft, H. & Tscharntke, T. 2018. Winners and losers of national and global efforts to reconcile agricultural intensification and biodiversity conservation. Global Change Biology 24(5): 2212–2228.

Ellenberg, H. & Mueller-Dombois, D. 1967. A key to Raunkiaer plant life forms with revised subdivisions. [s.n.], Göttingen.

Estudillo, J.P. & Otsuka, K. 2006. Lessons from three decades of Green Revolution in the Philippines. The Developing Economies 44(2): 123–148.

Evenson, R.E. & Gollin, D. 1997. Genetic Resources, International Organizations, and Improvement in Rice Varieties. Economic Development and Cultural Change 45(3): 471–500.

Fageria, N.K., Carvalho, G.D., Santos, A.B., Ferreira, E.P.B. & Knupp, A.M. 2011. Chemistry of Lowland Rice Soils and Nutrient Availability. Communications in Soil Science and Plant Analysis 42(16): 1913–1933.

FAO 2000. Bridging the rice yield gap in the Asia-Pacific region. FAO, Bangkok, Thailand.

FAO 2006. Guidelines for Soil Description. 4th ed. FAO, Rome, Italy.

FAO 2014. A regional rice strategy for sustainable food security in Asia and the Pacific. FAO, Bangkok, TH.

FAO 2016. Rice Market Monitor. URL: http://www.fao.org/economic/est/publications/rice-publications/rice-market-monitor-rmm/en/. Accessed 26 Jan 2017.

FAO 2020. FAOSTAT. URL: http://faostat.fao.org/. Accessed 6 Jan 2021.

Fernando, C.H. 1995. Rice fields are aquatic, semi-aquatic, terrestrial, and agricultural: A complex and questionable limnology. Tropical Limnology 1: 121–148.

Fischer, J., Lindenmayer, D.B. & Manning, A.D. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4(2): 80–86.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. 2011. Solutions for a cultivated planet. Nature 478: 337–342.

Fox, J. & Weisberg, S. 2019. An R companion to applied regression, 3rd ed. Sage, Thousand Oaks, US.

Fried, O., Kühn, I., Schrader, J., Nguyen V.S. & Bergmeier, E. 2017. Plant diversity and community composition of rice agroecosystems in Vietnam and the Philippines. Phytocoenologia 47(1): 49–66.

Fried, O., Kühn, I., Schrader, J., Nguyen, V.S. & Bergmeier, E. 2018. Plant diversity and composition of rice field bunds in Southeast Asia. Paddy and Water Environment 16(2): 359–378.

Fukamachi, K., Oku, H. & Miyake, A. 2005. The relationships between the structure of paddy levees and the plant species diversity in cultural landscapes on the west side of Lake Biwa, Shiga, Japan. Landscape and Ecological Engineering 1(2): 191–199.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. 2010. Weed species richness in winter wheat increases with landscape heterogeneity. Agriculture, Ecosystems & Environment 138(3-4): 318–323.

Gabriel, D., Thies, C. & Tscharntke, T. 2005. Local diversity of arable weeds increases with landscape complexity. Perspectives in Plant Ecology, Evolution and Systematics 7(2): 85–93.

Galinato, M.I., Moody, K. & Piggin, C.M. 1999. Upland rice weeds of South and Southeast Asia. International Rice Research Institute, Makati City, PH.

García, P.V. & Benzal, A.V. 2009. Flórula y vegetación de "Els Ullals de Na Molins" (La Albufera. Valencia). Referencia de un estado intermedio de restauración de humedales. Flora Montiberica 42: 31–40.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.-Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J. & Perfecto, I. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proceedings of the Royal Society B - Biological Sciences 281(1791): 20141358.

GRiSP 2013. Rice almanac. 4th ed. International Rice Research Institute, Los Baños, PH.

Harada, J., Paisooksantivatana, Y. & Zungsontiporn, S. 1987. Weeds in the highlands of northern Thailand. Color illustrated. 1st ed. National Weed Science Research Institute Project, c/o Botany and Weed Science Division, Dept. of Agriculture, Bangkok, TH.

Harada, J., Shibayama, H. & Morita, H. 1993. Weeds in the Tropics. Association for International Cooperation of Agriculture & Forestry, Tokyo, JP.

Hass, A.L., Liese, B., Heong, K.L., Settele, J., Tscharntke, T. & Westphal, C. 2018. Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. Agriculture, Ecosystems & Environment 253: 140–147.

Heckman, C.W. 1979. Rice field ecology in Northeastern Thailand. The effect of wet and dry seasons on a cultivated aquatic ecosystem. Kluwer Academic Publishers, Dordrecht, NL.

Hill, J.E. & Mortimer, A.M. 2001. Water and weed management in direct-seeded rice: are we headed in the right direction? In: Peng, S. & Hardy, B. (eds.) Rice research for food security and poverty alleviation: proceedings of the International Rice Research Conference, 31 March-3 April 2000, pp. 491–510, Los Baños, PH.

Hill, J.E., Smith, R.J., Jr. & Bayer, D.E. 1994. Rice weed control. Current technology and emerging issues in temperate rice. Australian Journal of Experimental Agriculture 34(7): 1021.

Hill, R. & Pickering, C. 2009. Differences in resistance of three subtropical vegetation types to experimental trampling. Journal of Environmental Management 90(2): 1305–1312.

Ho, P.-H. 1999-2003. Cayco Vietnam [An Illustrated Flora of Vietnam]. Vols. 1–3. Nha xuat ban tre [Mekong Printing], Ho Chi Minh City, VN.

Holm, L.G. 1977. The World's worst weeds. Distribution and biology. University Press of Hawaii, Honolulu, US.

Huang, H.-C., Liu, C.-W., Chen, S.-K. & Chen, J.-S. 2003. Analysis of percolation and seepage through paddy bunds. Journal of Hydrology 284(1): 13–25.

Huang, X., Kurata, N., Wei, X., Wang, Z.-X., Wang, A., Zhao, Q., Zhao, Y., Liu, K., Lu, H., Li, W., Guo, Y., Lu, Y., Zhou, C., Fan, D., Weng, Q., Zhu, C., Huang, T., Zhang, L., Wang, Y., Feng, L., Furuumi, H., Kubo, T., Miyabayashi, T., Yuan, X., Xu, Q., Dong, G., Zhan, Q., Li, C., Fujiyama, A., Toyoda, A., Lu, T., Feng, Q., Qian, Q., Li, J. & Han,

B. 2012. A map of rice genome variation reveals the origin of cultivated rice. Nature 490: 497–501.

Husson, O., Castella, J.-C., Ha Dinh Tuan & Naudin, K. 2001. Agronomic diagnosis and identification of factors limiting upland rice yield in mountainous areas of Northern Vietnam. SAM Paper Series 2, Vietnam Agricultural Institute, Hanoi, VN.

Hyvönen, T. & Salonen, J. 2002. Weed species diversity and community composition in cropping practices at two intensity levels – a six-year experiment. Plant Ecology 159(1): 73–81.

Ichihara, M., Matsuno, K., Inagaki, H., Saiki, C., Mizumoto, S., Yamaguchi, S., Yamashita, M. & Sawada, H. 2015. Creation of paddy levees to enhance the ecosystem service of weed seed predation by crickets. Landscape and Ecological Engineering 11(1): 227–233.

Iiyama, N., Kamada, M. & Nakagoshi, N. 2005. Ecological and social evaluation of landscape in a rural area with terraced paddies in southwestern Japan. Landscape and Urban Planning 70(3–4): 301–313.

Ikehashi, H. 2007. The Origin of Flooded Rice Cultivation. Rice Science 14(3): 161–171.

Inkscape Team 2015. Inkscape, version 0.91. Retrieved from http://www.inkscape.org.

IRRI 1983. Proceedings of the Conference on Weed Control in Rice. International Rice Research Institute, Los Baños, PH.

IRRI 2018. International Rice Genebank. URL: https://www.irri.org/international-rice-genebank. Accessed 11 Jan 2021.

IRRI 2020. Rice Knowledge Bank. URL: http://www.knowledgebank.irri.org/step-by-step-production/pre-planting/crop-calendar. Accessed 20 Feb 2020.

IUCN 2015. The IUCN Red List of Threatened Species. Version 2015-3. URL:http://www.iucnredlist.org. Accessed 9 Sept 2015.

Jaeger, B. 2017. R2glmm: computes R squared for mixed (multilevel) models, version 0.1.2. Retrieved from https://CRAN.R-project.org/package=r2glmm.

Jakobs, G., Kueffer, C. & Daehler, C.C. 2010. Introduced weed richness across altitudinal gradients in Hawai'i. Humps, humans and water-energy dynamics. Biological Invasions 12(12): 4019–4031.

José-María, L., Armengot, L., Blanco-Moreno, J.M., Bassa, M. & Sans, F.X. 2010. Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. Journal of Applied Ecology 47(4): 832–840.

Juraimi, A.S., Muhammad Saiful, A.H., Uddin, M.K., Anuar, A.R. & Azmi, M. 2011. Diversity of weed communities under different water regimes in bertam irrigated direct seeded rice field. Australian Journal of Crop Science 5(5): 595–604.

Kamoshita, A., Araki, Y. & Nguyen, Y.T.B. 2014. Weed biodiversity and rice production during the irrigation rehabilitation process in Cambodia. Agriculture, Ecosystems & Environment 194(0): 1–6.

Kamoshita, A., Ikeda, H., Yamagishi, J. & Ouk, M. 2010. Ecophysiological study on weed seed banks and weeds in Cambodian paddy fields with contrasting water availability. Weed Biology and Management 10(4): 261–272.

Kaspary, T.E., Roma-Burgos, N. & Merotto, A. 2020. Snorkeling Strategy: Tolerance to Flooding in Rice and Potential Application for Weed Management. Genes 11(9): 975.

Kawano, N., Kawano, K. & Ohsawa, M. 2009. Floristic diversity and the richness of locally endangered plant species of semi-natural grasslands under different management practices, southern Kyushu, Japan. Plant Ecology & Diversity 2(3): 277–288.

Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H. & Kuemmerle, T. 2017. Biodiversity at risk under future cropland expansion and intensification. Nature Ecology & Evolution 1(8): 1129–1135.

Khush, G.S. 1997. Origin, dispersal, cultivation and variation of rice. Plant Molecular Biology 35(1-2): 25–34.

Kim, J.W. & Nam, H.K. 1998. Syntaxonomical and synecological characteristic of rice field vegetation. Korean Journal of Ecology 21: 203–215.

Kim, S.C. & Ha, W.G. 2005. Direct-seeding and weed management in Korea. In: Toriyama, K., Heong, K.L. & Hardy, B. (eds.) Rice is life: scientific perspectives for the

21st century. Proceedings of the World Rice Research Conference held in Tokyo and Tsukuba, Japan, 4-7 November 2004, Los Baños, PH, Tsukuba, JP.

Kim, Y.M. 2001. Untersuchung von Flora, Vegetation und Biotoptypen in der dörflichen Kulturlandschaft Koreas. Studies on flora, vegetation and biotope types in Korean villages. Dissertation, Technische Universität Berlin, DE.

Klotz, S., Kühn, I. & Durka, W. 2002. BIOLFLOR. Eine Datebank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bundesamt für Naturschutz, Bonn-Bad Godesberg, DE.

Klotzbücher, T., Marxen, A., Vetterlein, D., Schneiker, J., Türke, M., Nguyen, V.S., Manh, N.H., Chien, H.V., Marquez, L., Villareal, S., Bustamante, J.V. & Jahn, R. 2015. Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. Basic and Applied Ecology 16(8): 665–673.

Kolbek, J., Dostálek, J. & Jarolímek, I. 1996. The vegetation of rice fields in North Korea and its relation to South Korea and Japan. Fragmenta Floristica et Geobotanica 41(2): 612–637.

Kontgis, C., Schneider, A. & Ozdogan, M. 2015. Mapping rice paddy extent and intensification in the Vietnamese Mekong River Delta with dense time stacks of Landsat data. Remote Sensing of Environment 169: 255–269.

Kosaka, Y., Xayvongsa, L., Vilayphone, A., Chanthavong, H., Takeda, S. & Kato, M. 2013. Wild Edible Herbs in Paddy Fields and Their Sale in a Mixture in Houaphan Province, the Lao People's Democratic Republic. Economic Botany 67(4): 335–349.

Koyanagi, T.F., Yamada, S., Yonezawa, K., Kitagawa, Y. & Ichikawa, K. 2014. Plant species richness and composition under different disturbance regimes in marginal grasslands of a Japanese terraced paddy field landscape. Applied Vegetation Science 17(4): 636–644.

Kraehmer, H., Jabran, K., Mennan, H. & Chauhan, B.S. 2016. Global distribution of rice weeds – A review. Crop Protection 80: 73–86.

Kudsk, P. & Streibig, J.C. 2003. Herbicides - a two-edged sword. Weed Research 43(2): 90–102.

Kumalasari, N.R. 2014. Diversity of rice weeds vegetation and its potential as local forage resource in Java, Indonesia. Dissertation, Georg-August-Universität Göttingen, DE.

Kumalasari, N.R., Abdullah, L. & Bergmeier, E. 2014. Nutrient assessment of paddy weeds as ruminant feed in Java. Livestock Research for Rural Development 26(4).

Kumalasari, N.R. & Bergmeier, E. 2014. Effects of surrounding crop and semi-natural vegetation on the plant diversity of paddy fields. Agriculture & Food Security 3(1): 15.

Kunin, W.E. 1998. Biodiversity at the edge. A test of the importance of spatial "mass effects" in the Rothamsted Park Grass experiments. Proceedings of the National Academy of Sciences 95(1): 207–212.

Landolt, E. 1999. Pleustonic communities with Lemnaceae in South America. Applied Vegetation Science 2(1): 7–16.

Le, K.B. 2007. Thuc vat chi viet nam [Flora of Vietnam]. Vol. 7. Ho cuc - Asteraceae Dumort. Science and Technics Publishing House, Ha Noi, VN.

Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129(2): 271–280.

Liang, K., Yang, T., Zhang, S., Zhang, J., Luo, M., Fu, L. & Zhao, B. 2016. Effects of intercropping rice and water spinach on net yields and pest control: an experiment in southern China. International Journal of Agricultural Sustainability 14(4): 448–465.

Lüdecke, D., Makowski, D. & Waggoner, P. 2020. performance: assessment of regression models performance, version 0.4.4. Retrieved from https://CRAN.R-project.org/ package=performance.

Luo, Y., Fu, H. & Traore, S. 2014. Biodiversity conservation in rice paddies in China: Toward ecological sustainability. Sustainability 6(9): 6107–6124.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. 2015. cluster: cluster analysis basics, version 2.0.3. Retrieved from https://cran.r-project.org/package=cluster.

Mahajan, G., Chauhan, B.S. & Kumar, V. 2014. Integrated weed management in rice. In: Chauhan, B.S. & Mahajan, G. (eds.) Recent advances in weed management, pp. 125–154. Springer New York, New York, US.

Maltchik, L., Rolon, A.S., Stenert, C., Machado, I.F. & Rocha, O. 2011. Can rice field channels contribute to biodiversity conservation in Southern Brazilian wetlands? Revista de Biología Tropical 59: 1895–1914.

Maltchik, L., Stenert, C. & Batzer, D.P. 2017. Can rice field management practices contribute to the conservation of species from natural wetlands? Lessons from Brazil. Basic and Applied Ecology 18: 50–56.

Martin, K. & Sauerborn, J. 2013. Agroecology. Springer Netherlands, Dordrecht, NL.

Martínez, E., Rös, M., Bonilla, M.A. & Dirzo, R. 2015. Habitat heterogeneity affects plant and arthropod species diversity and turnover in traditional cornfields. PLOS ONE 10(7): e0128950.

Maskell, L.C., Botham, M., Henrys, P., Jarvis, S., Maxwell, D., Robinson, D.A., Rowland, C.S., Siriwardena, G., Smart, S., Skates, J., Tebbs, E.J., Tordoff, G.M. & Emmett, B.A. 2019. Exploring relationships between land use intensity, habitat heterogeneity and biodiversity to identify and monitor areas of High Nature Value farming. Biological Conservation 231: 30–38.

Matsumura, T. & Takeda, Y. 2010. Relationship between species richness and spatial and temporal distance from seed source in semi-natural grassland. Applied Vegetation Science 13(3): 336–345.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. In: Prentice, I.C. & van der Maarel, Eddy (eds.) Theory and models in vegetation science, pp. 89–107. Springer Netherlands, Dordrecht, NL.

Miyawaki, A. 1960. Pflanzensoziologische Untersuchungen über Reisfeld-Vegetation auf den Japanischen Inseln mit vergleichender Betrachtung Mitteleuropas. Vegetatio Acta Geobot 9(6): 345–402.

Miyawaki, A. 1969. Systematik der Ackerunkrautgesellschaften Japans. Vegetatio 19(1-6): 47–59.

Miyawaki, A. 1988. Die Veränderung innerhalb der japanischen anthropogenen Vegetation. Flora 180: 191–201.

Molina, J., Sikora, M., Garud, N., Flowers, J.M., Rubinstein, S., Reynolds, A., Huang, P., Jackson, S., Schaal, B.A., Bustamante, C.D., Boyko, A.R. & Purugganan, M.D. 2011. Molecular evidence for a single evolutionary origin of domesticated rice. Proceedings of the National Academy of Sciences of the United States of America 108(20): 8351–8356.

Moody, K. 1989. Weeds reported in rice in South and Southeast Asia. International Rice Research Institute, Los Baños, PH.

Moody, K. & Drost, D.C. 1983. The role of cropping systems on weeds in rice. In: IRRI (ed.) Proceedings of the Conference on Weed Control in Rice, pp. 73–88, International Rice Research Institute, Los Baños, PH.

Morita, H. & Kabaki, N. 2002. Effects of soil moisture conditions on the emergence of weeds and rice plants from rainfed paddy soils in north-east Thailand. Weed Biology and Management 2(4): 209–212.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., García, R.G., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, Fred J. A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, Joop H. J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M. & Tichý, L. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264.

Mucina, L., Dostálek, J., Jarolímek, I., Kolbek, J. & Ostrý, I. 1991. Plant communities of trampled habitats in North Korea. Journal of Vegetation Science 2(5): 667–678.

Muthayya, S., Sugimoto, J.D., Montgomery, S. & Maberly, G.F. 2014. An overview of global rice production, supply, trade, and consumption. Annals of the New York Academy of Sciences 1324(1): 7–14.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772): 853–858.

Naito, R., Sakai, M. & Morimoto, Y. 2012. Negative effects of deep roadside ditches on Pelophylax porosa brevipoda dispersal and migration in comparison with Hyla japonica in a rice paddy area in Japan. Zoological Science 29(9): 599–603.

Naito, R., Sakai, M., Natuhara, Y., Morimoto, Y. & Shibata, S. 2013. Microhabitat use by Hyla japonica and Pelophylax porosa brevipoda at levees in rice paddy areas of Japan. Zoological Science 30(5): 386–391.

Naylor, R. 1994. Herbicide use in Asian rice production. World Development 22(1): 55–70.

Nemoto, M. & Otsuka, H. 2014. Influence of farming system on the floristic composition of paddy landscapes: a case study in a rural hilly zone in Zhejiang province, China. Landscape and Ecological Engineering 10(1): 173–180.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., Palma, A. de, Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W. & Purvis, A. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520: 45–50.

Nguyen, H.D. & Nguyen, T.D. 2007. Thuc vat chi viet nam [Flora of Vietnam]. Vol. 11. 1. Bo rong mo - Fucales Kylin 2. Ho rau ram - Polygonaceae Juss. Science and Technics Publishing House, Ha Noi, VN.

Nguyen, K.K. 2002. Thuc vat chi viet nam [Flora of Vietnam]. Vol. 3. Ho coi - Cyperaceae Juss. Science and Technics Publishing House, Ha Noi, VN.

Nguyen, V.S., Nguyen, H.M., Klotzbücher, A., Vetterlein, D., Klotzbücher, T., Jahn, R., Schneiker, J., Türke, M., Fried, O., Bergmeier, E., Sattler, C. & Settele, J. 2018. From science to application. Field demonstrations to enhance sustainable rice production in the north of Vietnam - Lessons from the LEGATO project. Paddy and Water Environment: 1–6.

Ning, C., Qu, J., He, L., Yang, R., Chen, Q., Luo, S. & Cai, K. 2017. Improvement of yield, pest control and Si nutrition of rice by rice-water spinach intercropping. Field Crop Research 208: 34–43.

Nithya, J. & Ramamoorthy, D. 2015. Floristic composition and weed diversity in rice fields. Indian Journal of Weed Science 47(4): 417–421.

Nowak, A., Nowak, S. & Nobis, M. 2015. First insights into weed communities of rice agrocoenoses in southern Thailand. Phytocoenologia 45(1): 157–174.

Nowak, A., Nowak, S. & Nobis, M. 2016. Spring weed communities of rice agrocoenoses in central Nepal. Acta Botanica Croatica 75(1): 99–108.

Nowak, S., Nowak, A. & Nobis, M. 2013. Weed communities of rice fields in the central Pamir Alai Mountains (Tajikistan, Middle Asia). Phytocoenologia 43(1-2): 101–126.

Oerke, E.-C. & Dehne, H.-W. 2004. Safeguarding production – losses in major crops and the role of crop protection. Crop Protection 23(4): 275–285.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. 2019. vegan: community ecology package, version 2.5-4. Retrieved from http://CRAN.R-project.org/package=vegan.

Otsuka, H., Nemoto, M. & Masuda, S. 2006. The floristic composition of paddy fields and their levees under different weed management techniques [in Japanese with English Summary]. Journal of Weed Science and Technology 51(4): 229–238.

Pancho, J.V. & Obien, S.R. 1995. Manual of ricefield weeds in the Philippines. Philippine Rice Research Institute, Muñoz, PH.

Parras, J.M.M. & Lorca, M.P. 1993. Vegetación de los arrozales de las marismas del Guadalquivir. Lagascalia 17(1): 21–35.

Paudel, M.N. 2011. Rice (Oryza sativa L) cultivation in the highest elevation of the world. Agronomy Journal of Nepal 2: 31–41.

Piccoli, F. & Gerdol, R. 1981. Rice-field weed communities in Ferrara Province (northern Italy). Aquatic Botany 10: 317–328.

Pingali, P.L. 2012. Green Revolution: Impacts, limits, and the path ahead. Proceedings of the National Academy of Sciences of the United States of America 109(31): 12302–12308.

Pingali, P.L. & Xuan, V.-T. 1992. Vietnam: Decollectivization and rice productivity growth. Economic Development and Cultural Change 40(4): 697–718.

Pinke, G., Csiky, J., Mesterházy, A., Tari, L., Pál, R.W., Botta-Dukát, Z. & Czúcz, B. 2014. The impact of management on weeds and aquatic plant communities in Hungarian rice crops. Weed Research 54(4): 388–397.

Piras, E. 2011. Reis ist Leben. Wie Öko-Landbau und Fairer Handel zu Ernährungssouveränität führen. URL: https://www.naturland.de/de/naturland/publikationen.html. Accessed 3 Dec 2012.

Poggio, S.L., Chaneton, E.J. & Ghersa, C.M. 2013. The arable plant diversity of intensively managed farmland. Effects of field position and crop type at local and landscape scales. Agriculture, Ecosystems & Environment 166: 55–64.

Poos, M.S. & Jackson, D.A. 2012. Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. Ecological Indicators 18: 82–90.

Pretty, J.N. 2002. Agri-Culture. Reconnecting people, land and nature. Earthscan Publications Ltd, London, UK.

Pu, D., Shi, M., Wu, Q., Gao, M., Liu, J.-F., Ren, S., Yang, F., Tang, P., Ye, G., Shen, Z., He, J., Yang, D., Bu, W.-J., Zhang, C., Song, Q., Xu, D., Strand, M.R. & Chen, X. 2014. Flower-visiting insects and their potential impact on transgene flow in rice. Journal of Applied Ecology 51(5): 1357–1365.

Pyšek, P. & Lepš, J. 1991. Response of a weed community to nitrogen fertilization: a multivariate analysis. Journal of Vegetation Science 2(2): 237–244.

R Core Team 2018. R: A language and environment for statistical computing, version 3.5.2. Retrieved from https://www.R-project.org/.

Raju, R.A., Reddy, M.N. & Gangwar, B. 2001. Nursery fertilization of rice (Oryza sativa) with native weed vegetation. Indian Journal of Agronomy 1(46): 94–100.

Rao, A.N., Johnson, D.E., Sivaprasad, B., Ladha, J.K. & Mortimer, A.M. 2007. Weed Management in Direct-Seeded Rice. In: Sparks, D.L. (ed.) Advances in Agronomy, pp. 153–255. Elsevier Academic Press Inc., San Diego, US.

Reichelt, G. & Wilmanns, O. 1973. Vegetationsgeographie. Westermann, Braunschweig, DE.

Rivas-Martinez, S. & Rivas-Saenz, S. 1996-2009. Worldwide Bioclimatic Classification System. URL: http://www.globalbioclimatics.org/. Accessed 22 Sept 2015.

Roder, W. 1997. Slash-and-burn rice systems in transition: challenges for agricultural development in the hills of Northern Laos. Mountain Research and Development 17(1): 1–10.

Roder, W., Phengchanh, S. & Keobulapha, B. 1997. Weeds in slash-and-burn rice fields in northern Laos. Weed Research 37(2): 111–119.

Roschewitz, I., Gabriel, D., Tscharntke, T. & Thies, C. 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. Journal of Applied Ecology 42(5): 873–882.

Roskov, Y., Abucay, L., Orrell, T., Nicolson, D., Kunze, T., Flann, C., Bailly, N., Kirk, P., Bourgoin, T., DeWalt, R.E., Decock, W. & Wever, A. de (eds.) 2015. Species 2000 & ITIS Catalogue of Life. URL: https://www.catalogueoflife.org/col/. Accessed 23 Dec 2015.

Rossi, G., Tazzari, E.R., Abeli, T., Cauzzi, P., Ardenghi, N., Orsenigo, S. & Vagge, I. 2015. Activities and perspectives of plant diversity conservation in rice paddies (and surrounding) of Po River Plain, N-Italy Second organic rice farming and production systems international conference, pp. 114–115.

Sanchez, P.L., Wing, R.A. & Brar, D.S. 2013. The wild relative of rice: Genomes and genomics. In: Zhang, Q. & Wing, R.A. (eds.) Genetics and genomics of rice, pp. 9–25. Springer New York, New York, US.

Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecologica 23(3): 137–154.

Schoenly, K., Cohen, J.E., Heong, K.L., Litsinger, J.A., Aquino, G.B., Barrion, A.T. & Arida, G. 1996. Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. Bulletin of Entomological Research 86(4): 451–466.

Schrader, J., Franzén, M., Sattler, C., Ferderer, P. & Westphal, C. 2018. Woody habitats promote pollinators and complexity of plant–pollinator interactions in homegardens located in rice terraces of the Philippine Cordilleras. Paddy and Water Environment 16(2): 253–263.

Settele, J., Heong, K.L., Kühn, I., Klotz, S., Spangenberg, J.H., Arida, G., Beaurepaire, A., Beck, S., Bergmeier, E., Burkhard, B., Brandl, R., Bustamante, J.V., Butler, A., Cabbigat, J., Le, X.C., Catindig, J.L.A., van Ho, C., Le, Q.C., Dang, K.B., Escalada, M., Dominik, C., Franzén, M., Fried, O., Görg, C., Grescho, V., Grossmann, S., Gurr, G.M., Hadi, B.A.R., Le, H.H., Harpke, A., Hass, A.L., Hirneisen, N., Horgan, F.G., Hotes, S., Isoda, Y., Jahn, R., Kettle, H., Klotzbücher, A., Klotzbücher, T., Langerwisch, F., Loke, W.-H., Lin, Y.-P., Lu, Z., Lum, K.-Y., Magcale-Macandog, D.B., Marion, G., Marquez, L., Müller, F., Nguyen, H.M., Nguyen, Q.A., Nguyen, V.S., Ott, J., Penev, L., Pham, H.T., Radermacher, N., Rodriguez-Labajos, B., Sann, C., Sattler, C., Schädler, M., Scheu, S., Schmidt, A., Schrader, J., Schweiger, O., Seppelt, R., Soitong, K., Stoev, P., Stoll-Kleemann, S., Tekken, V., Thonicke, K., Tilliger, B., Tobias, K., Andi Trisyono, Y., Dao, T.T., Tscharntke, T., Le, Q.T., Türke, M., Václavík, T., Vetterlein, D., Villareal, S., Vu, K.C., Vu, Q., Weisser, W.W., Westphal, C., Zhu, Z. & Wiemers, M. 2018. Rice ecosystem services in South-east Asia. Paddy and Water Environment 16(2): 211–224.

Settele, J., Kühn, I., Klotz, S., Arida, G., Bergmeier, E., Burkhard, B., Bustamante, J.V., Dao Thanh Truong, Escalada, M., Görg, C., Grescho, V., Ho Van Chien, Heong, K.L., Hirneisen, N., Hotes, S., Jahn, R., Klotzbücher, T., Marion, G., Marquez, L., Marxen, A., Moritz, R., Müller, F., Nguyen V.S., Ott, J., Penev, L., Rodriguez-Labajos, B., Schädler, M., Scheu, S., Seppelt, R., Stoev, P., Tscharntke, T., Tekken, V., Thonicke, K., Vetterlein, D., Vidal, S., Villareal, S., Weisser, W.W., Westphal, C., Wiemers, M. & Spangenberg, J.H. 2013. Kulturlandschaftsforschung in Südostasien – das LEGATO-Projekt. Berichte, Geographie und Landeskunde 87(3): 315–323.

Settele, J., Spangenberg, J.H., Heong, K.L., Burkhard, B., Bustamante, J.V., Cabbigat, J., Chien, H.V., Escalada, M., Grescho, V., Le Hai, H., Harpke, A., Horgan, F.G., Hotes,

S., Jahn, R., Kühn, I., Marquez, L., Schädler, M., Tekken, V., Vetterlein, D., Villareal, S., Westphal, C. & Wiemers, M. 2015. Agricultural landscapes and ecosystem services in South-East Asia—the LEGATO-Project. Basic and Applied Ecology 16(8): 661–664.

Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D. & Lestari, A.S. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77(7): 1975.

Shmida, A. & Wilson, M.V. 1985. Biological determinants of species diversity. Journal of Biogeography 12: 1–20.

Singh, S. & Singh, M. 2009. Effect of temperature, light and pH on germination of twelve weed species. Indian Journal of Weed Science 41(3&4): 113–126.

Smith, R.J., Jr. 1983. Weeds of major economic importance in rice and yield losses due to weed competition. In: IRRI (ed.) Proceedings of the Conference on Weed Control in Rice, pp. 19–36, International Rice Research Institute, Los Baños, PH.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P. & Brook, B.W. 2010. The state and conservation of Southeast Asian biodiversity. Biodiversity and Conservation 19(2): 317–328.

Soerjani, M., Kostermans, A.J.G.H. & Tjitrosoepomo, G. 1987. Weeds of rice in Indonesia. Balai Pustaka, Jakarta, ID.

Sowattanangoon, N., Kotchabhakdi, N. & Petrie, K.J. 2009. The influence of Thai culture on diabetes perceptions and management. Diabetes Research and Clinical Practice 84(3): 245–251.

Sterling, E.J., Hurley, M.M., Le, M.D. & Powzyk, J.A. 2008. Vietnam. A natural history. Yale University Press, New Haven, US.

Tallon, G. 1958. La flore des rizieres de la region d'arles et ses repercussions sur la culture du riz. Vegetatio 8(1): 20–42.

Tanaka, I. 1976. Climatic influence on photosynthesis and respiration of rice plants. In: IRRI (ed.) Climate and rice, pp. 223–247, International Rice Research Institute, Los Baños, PH.

Tassin, J. & Rivière, J.-N. 2003. Gradient altitudinal de richesse en plantes invasives à l'île de La Réunion (archipel des Mascareignes, océan Indien). Revue d'écologie 58(3): 257–270.

Tekken, V. & Settele, J. 2014. Instrumente zur nachhaltigen Agrarlandschafts-Optimierung. Ecological Engineering als Ansatz zur Konstruktion nachhaltiger Agrarlandschaften in Reisanbaugebieten Südost-Asiens. In: Hartung, G. & Kirchhoff, T. (eds.) Welche Natur brauchen wir? Analyse einer anthropologischen Grundproblematik des 21. Jahrhunderts, pp. 173–186. Verlag Karl Alber, Freiburg/München, DE.

The Plant List 2013. Version 1.1. URL: http://www.theplantlist.org/. Accessed 6 Mar 2016.

Tichý, L. 2002. JUICE, software for vegetation classification. Journal of Vegetation Science 13(3): 451–453.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. & Polasky, S. 2002. Agricultural sustainability and intensive production practices. Nature 418(6898): 671–677.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. & Packer, C. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546: 73–81.

Tomita, S., Nawata, E., Kono, Y., Nagata, Y., Noichana, C., Sributta, A. & Inamura, T. 2003. Differences in weed vegetation in response to cultivating methods and water conditions in rainfed paddy fields in north-east Thailand. Weed Biology and Management 3(2): 117–127.

Tran, T.U. & Kajisa, K. 2006. The impact of Green Revolution on rice production in Vietnam. The Developing Economies 44(2): 167–189.

Tsiripidis, I., Bergmeier, E., Fotiadis, G. & Dimopoulos, P. 2009. A new algorithm for the determination of differential taxa. Journal of Vegetation Science 20(2): 233–240.

Tuomisto, H. 2010a. A diversity of beta diversities. Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33(1): 2–22.

Tuomisto, H. 2010b. A diversity of beta diversities. Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33(1): 23–45.

Tuong, P., Bouman, B. & Mortimer, M. 2005. More rice, less water – Integrated approaches for increasing water productivity in irrigated rice-based systems in Asia. Plant Production Science 8(3): 231–241.

Turki, Z. & Sheded, M. 2002. Some observations on the weed flora of rice fields in the Nile Delta, Egypt. Feddes Repertorium 113(5-6): 394–403.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. 2010. Conservation of species interaction networks. Biological Conservation 143(10): 2270–2279.

United Nations, Department of Economic and Social Affairs, Population Division 2017. World Population Prospects: The 2017 Revision, Key findings and Advance Tables. Working Paper No. ESA/P/WP/248, New York, US.

Vân, N.K. 2016. Climatic zoning of the Bac Bo mountainous provinces and Western Thanh Nghe. [In Vietnamese with English summary]. Vietnam Journal of Earth Sciences 37(3): 204–212.

Way, M.J. & Heong, K.L. 1994. The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice – a review. Bulletin of Entomological Research 84(4): 567–587.

Webster, E. 2014. Weed management. In: Saichuk, J. (ed.) Lousiana rice production handbook. Pub 2321, pp. 54–81. Louisiana State University Agricultural Center, Baton Rouge, US.

Westphal, C., Vidal, S., Horgan, F.G., Gurr, G.M., Escalada, M., Chien, H.V., Tscharntke, T., Heong, K.L. & Settele, J. 2015. Promoting multiple ecosystem services with flower strips and participatory approaches in rice production landscapes. Basic and Applied Ecology 16(8): 681–689.

Williams, J.F., Roberts, S.R., Hill, J.E., Scardaci, S.C. & Tibbits, G. 1990. IPM: managing water for weed control in rice. California Agriculture 44(5): 7–10.

Wittig, R., Becker, U. & Ataholo, M. 2011. Weed communities of arable fields in the Sudanian and the Sahelian zone of West Africa. Phytocoenologia 41(2): 107–164.

Yamada, S., Kusumoto, Y., Tokuoka, Y. & Yamamoto, S. 2011. Landform type and land improvement intensity affect floristic composition in rice paddy fields from central Japan. Weed Research 51(1): 51–62.

Yamada, S., Okubo, S., Kitagawa, Y. & Takeuchi, K. 2007. Restoration of weed communities in abandoned rice paddy fields in the Tama Hills, central Japan. Agriculture, Ecosystems & Environment 119(1–2): 88–102.

Yasuda, M., Takeda, A., Tabuchi, K., Yasuda, T. & Watanabe, T. 2013. Effects of Japanese rice field boundary vegetation on Stenotus rubrovittatus (Hemiptera: Miridae) abundance. Applied Entomology and Zoology 48(3): 289–294.

Yorks, T.P., West, N.E., Mueller, R.J. & Warren, S.D. 1997. Toleration of traffic by vegetation: Life form conclusions and summary extracts from a comprehensive data base. Environmental Management 21(1): 121–131.

Zedler, J.B. & Kercher, S. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23(5): 431–452.

Zhou, W., Lee, M.-B. & Goodale, E. 2018. The relationship between the diversity of herbaceous plants and the extent and heterogeneity of croplands in noncrop vegetation in an agricultural landscape of south China. Global Ecology and Conservation 14: e00399.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1(1): 3–14.

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List of publications

Peer-reviewed journal publications

König, P. & **Fried, O.** (2015): Plant communities on the NE coast of Oman and their site conditions. *Phytocoenologia* 45(3): 269-290. https://doi.org/10.1127/phyto/2015/0027

Fried, O., Schrader, J., Kühn, I., Nguyen V.S. & Bergmeier, E. (2017): Plant diversity and community composition of rice agroecosystems in Vietnam and the Philippines. *Phytocoenologia* 47(1): 49-66. https://doi.org/10.1127/phyto/2017/0123

Fried, O., Kühn, I., Schrader, J., Nguyen, V.S. & Bergmeier, E. (2018): Plant diversity and composition of rice field bunds in Southeast Asia. *Paddy and Water Environment* 16(2): 359-378. https://doi.org/10.1007/s10333-018-0657-8

Nguyen, V.S., Nguyen, H.M., Klotzbücher, A., Vetterlein, D., Klotzbücher, T., Jahn, R., Schneiker, J., Türke, M., **Fried, O.**, Bergmeier, E., Görg, C. & Settele, J. (2018): From science to application: Field demonstrations to enhance sustainable rice production in the North of Vietnam - Lessons from the LEGATO project. *Paddy and Water Environment* 16(2): 353-358. https://doi.org/10.1007/s10333-018-0644-0

Settele, J., Heong, K.L., Kühn, I., Klotz, S., Spangenberg, J.H., Arida, G., Beaurepaire, A., Beck, S., Bergmeier, E., Burkhard, B., Brandl, R., Bustamante, J.V., Butler, A., Cabbigat, J., Le, X.C., Catindig, J.L.A., van Ho, C., Le, Q.C., Dang, K.B., Escalada, M., Dominik, C., Franzén, M., **Fried, O.**, Görg, C., Grescho, V., Grossmann, S., Gurr, G.M., Hadi, B.A.R., Le, H.H., Harpke, A., Hass, A.L., Hirneisen, N., Horgan, F.G., Hotes, S., Isoda, Y., Jahn, R., Kettle, H., Klotzbücher, A., Klotzbücher, T., Langerwisch, F., Loke, W.-H., Lin, Y.-P., Lu, Z., Lum, K.-Y., Magcale-Macandog, D.B., Marion, G., Marquez, L., Müller, F., Nguyen, H.M., Nguyen, Q.A., Nguyen, V.S., Ott, J., Penev, L., Pham, H.T., Radermacher, N., Rodriguez-Labajos, B., Sann, C., Sattler, C., Schädler, M., Scheu, S., Schmidt, A., Schrader, J., Schweiger, O., Seppelt, R., Soitong, K., Stoev, P., Stoll-Kleemann, S., Tekken, V., Thonicke, K., Tilliger, B., Tobias, K., Andi Trisyono, Y., Dao, T.T., Tscharntke, T., Le, Q.T., Türke, M., Václavík, T., Vetterlein, D., Villareal, S., Vu, K.C., Vu, Q., Weisser, W.W., Westphal, C., Zhu, Z. & Wiemers, M. (2018): Rice ecosystem services in Southeast Asia. *Paddy and Water Environment* 16(2): 211-224. https://doi.org/10.1007/s10333-018-0656-9

Fried, O., Westphal, C., Schellenberg, J., Grescho, V., Kühn, I., Nguyen V.S., Settele, J. & Bergmeier, E.: Vascular plant species diversity in Southeast Asian rice ecosystems is

determined by climate and soil conditions as well as the proximity of non-paddy habitats. Accepted on 21st Jan 2021 in *Agriculture, Ecosystems and Environment*.

Conferences (selected list)

Fried, O., Bergmeier, E., Großmann, S., Kühn, I. & Nguyen, V.S. (2012): Species and life form composition of vascular plants in rice-based production systems. The 42nd Annual Conference of GfÖ (Gesellschaft für Ökologie). University of Lüneburg, Germany.

Fried, O., Bergmeier, E., Großmann, S., Kühn, I. (2012): Functional diversity in the vegetation of landscapes with different agricultural intensity. LEGATO-Workshop – Effects of land use on species and functional biodiversity and ecosystem services. University of Göttingen, Germany.

Fried, O., Bergmeier, E., Kühn, I., Nguyen, V.S. & Großmann, S. (2014): Phytodiversity in rice-based production systems. LEGATO: Ecological engineering in Asian rice landscapes, Ho Chi Minh City, Vietnam.

Fried, O., Bergmeier, E., Kühn, I., Nguyen, V.S. & Großmann, S. (2014): Vegetation of rice agroecosystems in the LEGATO regions. Rice Ecosystem Services in South-East Asian Landscapes - a LEGATO conference, Yogyakarta, Indonesia.

Appendix A

The contents of Appendix A can be found on the CD accompanying this thesis or in the internet following the corresponding URLs.

A.1: Description of the plant life forms (adapted from Ellenberg & Mueller-Dombois 1967) that were encountered in Southeast Asian rice paddies and/or on their bunds during the years 2012 to 2015.
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.2: Ordered relevé table of paddy cluster C1 (relevés 1-11: subunit C1a, relevés 12-27: subunit C1b, relevés 28-33: subunit C1c; DC1 = positive differential species of C1; * = exclusively differential species of C1).
Available on URL: *https://doi.org/10.1127/phyto/2017/0123*.

A.3: Ordered relevé table of paddy clusters C2 and C3 (relevés 69-97: C2, relevés 98-102: C3; DC2/3 = positive differential species of C2/3; * = exclusively differential species of particular cluster).
Available on URL: *https://doi.org/10.1127/phyto/2017/0123*.

A.4: Ordered relevé table of paddy cluster C4 (relevés 34-42: subunit C4a, relevés 43-52: subunit C4b, relevés 53-67: subunit C4c; DC4 = positive differential species of C4; * = exclusively differential species of C4).
Available on URL: *https://doi.org/10.1127/phyto/2017/0123*.

A.5: List of taxa found in Southeast Asian rice landscapes during the years 2012 to 2015 with their status in The IUCN Red List of Threatened Species (IUCN 2015), plant life form (PLF; Ch = chamaephytes, H = hemicryptophytes, G = geophytes, T = therophytes, Hel = helophytes, Hyd = hydrophytes, L = lianas/vines), growth form (PGF) and kind of usage (fert = fertilizer, ind = industry, med = medicine, orna = ornamental plant). Species counted in our index "Sipo" (marked as entomophilous) have showy flowers or are known from scientific literature (e.g. eFloras 2008) for being insect-pollinated.

A.6: UPGMA-generated classification dendrogram of the relevés collected in Vietnamese and Philippine rice paddies (Agglomerative Coefficient = 0.5).
Available on URL: *https://doi.org/10.1127/phyto/2017/0123*.

A.7: The paddy vegetation was surveyed in seven regions with varying levels of landscape heterogeneity. Communities C2 and C3 were restricted to intensive rice production sites like the vast monoculture areas in region PH2 (a). Communities C1 and C4 were more widespread, occurring mostly in lowland sites with intermediate landscape heterogeneity or highly heterogeneous mountain landscapes like in region PH3 (b). A detail of the C1c subunit growing in a paddy in PH3 (c), and of the C2 community from PH2 (d).
Available on URL: *https://doi.org/10.1127/phyto/2017/0123*.

A.8: Ordered relevé table of bunds clusters A1 and A2. Main diagnostic species in bold letters. Cover values of species show the mean percentage of the five subplots of each relevé after transformation from the Braun-Blanquet scale. Abbreviations of soil textural classes according to FAO (2006), pH = soil acidity, EC = electrical conductivity.
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.9: Ordered relevé table of bunds clusters B3 and B4. Main diagnostic species in bold letters. Cover values of species show the mean percentage of the five subplots of each relevé after transformation from the Braun-Blanquet scale. Abbreviations of soil textural classes according to FAO (2006), pH = soil acidity, EC = electrical conductivity.
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.10: Ordered relevé table of bunds clusters C5 and C6. Main diagnostic species in bold letters. Cover values of species show the mean percentage of the five subplots of each relevé after transformation from the Braun-Blanquet scale. Abbreviations of soil textural classes according to FAO (2006), pH = soil acidity, EC = electrical conductivity.
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.11: Farmers of the surveyed rice fields were interviewed on timing and practice of weed control. The number of rice field bunds that are subject to the applied methods varies between clusters, countries and altitudinal levels. (*One of the rice field bunds in VN4 was covered with plastic foil.)
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.12: UPGMA-generated classification dendrogram of the relevés collected on Southeast Asian rice field bunds (Agglomerative Coefficient = 0.41).
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.13: Comparison of bunds and adjacent paddies (cf. Fried et al. 2017) in Vietnam and the Philippines in terms of sampling effort, representative plot sizes, species richness (*S*), herb cover and life form composition.
Available on URL: *https://doi.org/10.1007/s10333-018-0657-8*.

A.14: Correlation matrix of variables recorded on bunds. Numbers represent Pearson's correlation coefficient.

A.15: Correlation matrix of variables recorded in paddies. Numbers represent Pearson's correlation coefficient.

A.16: Type III Analysis of Variance Table with Satterthwaite's method of variables with significant effects on plant species richness (*S*), Shannon index (*H*) and the number of entomophilous plants (S_{ipo}) on Southeast Asian rice field bunds (n = 123) and paddies (n = 110). *P*-values are based on *F*-statistics.

A.17: Effect sizes (% explained variances and R^2) of the models and corresponding predictor variables. R^2 is given for the entire model and for the fixed terms, respectively. Explained variance of random terms is corresponding to random variance of final model.

A.18: Generalized model predictions of the effects of surrounding landscape, mean annual temperature and soil acidity on the species richness of studied rice field bunds, based on linear mixed-effects models.

A.19: Generalized model predictions (based on linear mixed-effects models with dotted lines showing 95% confidence intervals) of the effects of mean annual temperature and surrounding landscape on species richness of Southeast Asian rice field bunds. Species richness decreases with mean annual temperature, in particular if bunds belong to monoculture sites. Points represent original data points.

A.20: Generalized model predictions (based on linear mixed-effects models with dotted lines showing 95% confidence intervals) of the effects of soil pH and surrounding landscape on regional species richness on bunds. Overall, decreasing soil acidity

enhanced species richness, but regional differences and the effect of surrounding landscape were more conspicuous. Points represent original data points.

A.21: The study regions (for full names see Fig. 1.7) were characterized by distinct levels of plot-level plant diversity (a) on bunds and (b) in paddies. Significant differences ($p < 0.05$) of Shannon diversity (H) between regions are indicated with letters ($n_{bunds} = 123$ and $n_{paddies} = 110$).

A.22: The study regions (for full names see Fig. 1.7) were characterized by distinct levels of plot-level plant diversity (a) on bunds and (b) in paddies. Significant differences ($p < 0.05$) of the number of entomophilous plants (S_{ipo}) between regions are indicated with letters ($n_{bunds} = 123$ and $n_{paddies} = 110$).

A.23: DCA ordination depicting plant community composition in paddies and their bunds. Site scores of the DCA ordination are shown along axes 1 (eigenvalue 0.50) and 2 (eigenvalue 0.37). Symbol sizes indicate the species richness at sites. The total inertia was 9.72.

Appendix B

B.1: The data sheet used for the vegetation survey

N°	Date:	Name:	Size:	Coordinates:		
Plot-ID / Location:			Description and history of plot:			
Exposition:	Slope:	Altitude:	Soil texture:		Rock fragments:	
Total cover:	Max. total height:	Stage of crop:		Crop cover:	Max. crop height:	
Herb cover:	Max. herb height:	Crop establishment:		direct seeding transplanting	Soil moisture / Water level:	

Species	Layer cover				Dev. stage	Collected
	Total	T	S	H		
1						
2						
3						
4						
5						
6						
7						
8						
9						
10						
11						
12						
13						
14						
15						
16						
17						

B.2: The standardized questionnaire used for the interviews

Date:_____

Questionnaire on the management of the paddies and their bunds

data requirements of WP 2.1.2. (Oliver Fried)

Name of farmer:_____ Transplanting Date:_____

Field-ID:_____

1. Which management methods are applied for the control of weeds on the **bunds**?

   - ☐ Trowel/Removing of top soil with vegetation
   - ☐ Cutting
   - ☐ Mulching/ Putting mud from paddy on bunds to cover the weeds
   - ☐ Herbicide-use
     →Name of herbicide: _____
   - ☐ Grazing
     →Name of animal:_____
   - ☐ Hand-weeding
   - ☐ Other:_____
   - ☐ None

2. When and how often are these methods applied?

3. Which management methods for the control of weeds on the **paddies**?

   - ☐ Grazing
     → Name of animal:_____
   - ☐ Herbicide-use
     →Name of herbicide: _____
   - ☐ Hand-weeding
   - ☐ Plowing
   - ☐ Harrowing
   - ☐ Other :_____
   - ☐ None

4. When and how often are these methods applied?

5. The paddy is flooded from _____ to_____

6. How many rice cultivation cycles per year? _____

Appendix C

The contents of Appendix C can be found on the CD accompanying this thesis.

PDF file of the present thesis

Fried_2021_Thesis_final.pdf

Fried, O. (2021): Plant community composition and biodiversity of irrigated rice ecosystems in Vietnam and the Philippines

PDF files of publications related to this dissertation

Fried_et_al_2017.pdf

Fried, O., Schrader, J., Kühn, I., Nguyen V.S. & Bergmeier, E. (2017): Plant diversity and community composition of rice agroecosystems in Vietnam and the Philippines. *Phytocoenologia* 47(1): 49-66. https://doi.org/10.1127/phyto/2017/0123

Fried_et_al_2018.pdf

Fried, O., Kühn, I., Schrader, J., Nguyen, V.S. & Bergmeier, E. (2018): Plant diversity and composition of rice field bunds in Southeast Asia. *Paddy and Water Environment* 16(2): 359-378. https://doi.org/10.1007/s10333-018-0657-8

Nguyen_et_al_2018.pdf

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Settele_et_al_2018.pdf

Settele, J., Heong, K.L., Kühn, I., Klotz, S., Spangenberg, J.H., Arida, G., Beaurepaire, A., Beck, S., Bergmeier, E., Burkhard, B., Brandl, R., Bustamante, J.V., Butler, A., Cabbigat, J., Le, X.C., Catindig, J.L.A., van Ho, C., Le, Q.C., Dang, K.B., Escalada, M., Dominik, C., Franzén, M., Fried, O., Görg, C., Grescho, V., Grossmann, S., Gurr, G.M., Hadi, B.A.R., Le, H.H., Harpke, A., Hass, A.L., Hirneisen, N., Horgan, F.G., Hotes, S., Isoda, Y., Jahn, R., Kettle, H., Klotzbücher, A., Klotzbücher, T., Langerwisch, F., Loke, W.-H., Lin, Y.-P., Lu, Z., Lum, K.-Y., Magcale-Macandog, D.B., Marion, G., Marquez, L., Müller, F., Nguyen, H.M., Nguyen, Q.A., Nguyen, V.S., Ott, J., Penev, L., Pham, H.T., Radermacher, N., Rodriguez-Labajos, B., Sann, C., Sattler, C., Schädler, M., Scheu, S., Schmidt, A., Schrader, J., Schweiger, O., Seppelt, R., Soitong, K., Stoev, P., Stoll-Kleemann, S., Tekken, V., Thonicke, K., Tilliger, B., Tobias, K., Andi Trisyono, Y., Dao, T.T., Tscharntke, T., Le, Q.T., Türke, M., Václavík, T., Vetterlein, D., Villareal, S., Vu, K.C., Vu, Q., Weisser, W.W., Westphal, C., Zhu, Z. & Wiemers, M. (2018): Rice ecosystem services in Southeast Asia. *Paddy and Water Environment* 16(2): 211-224. https://doi.org/10.1007/s10333-018-0656-9

Fried_et_al_2021.pdf

Fried, O., Westphal, C., Schellenberg, J., Grescho, V., Kühn, I., Nguyen, V.S., Settele, J. & Bergmeier, E.: Vascular plant species diversity in Southeast Asian rice ecosystems is determined by climate and soil conditions as well as the proximity of non-paddy habitats. Accepted on 21st Jan 2021 in *Agriculture, Ecosystems and Environment*.

Erklärung

Hiermit bestätige ich die vorliegende Dissertationsschrift ohne fremde Hilfe selbstständig verfasst und nur die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Göttingen, den 15.04.2021